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Edited by

CARLETON REA and J. RAMSBOTTOM

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THE ARUNDEL FORAY.

THE 1926 Spring Foray was held at Arundel from Friday evening, May 21st, to Tuesday morning, May 25th, with headquarters at the Norfolk Hotel. On Saturday, May 22nd, a start was made about 10.0 a.m. and the whole day was spent in working through Paine's Wood and Rewell Wood under the guidance of the Head Forester of the Norfolk estate. These woods lie to the west of Arundel, and consist mainly of oak and sweet chestnut, with some beech and occasional conifers. Large fungi were scarce, but a fair collection of the lower Basidiomycetes and of micro-fungi was obtained. Mr Pearson secured *Tulasnella* (*Glocotulasnella*) *cystidiophora* v. Hoehn. & Litsch., which will be described by him in a separate paper. Other interesting finds were *Collybia leucomyosotis*, *Peniophora longispora* (a very fine specimen), an unusually large specimen of *Ganoderma applanatum*, *Eichleriella spinulosa*, *Bourdotia Eyrei** with its characteristic red coloration of beech wood, and *Hypocrea fungicola* on an old specimen of *Polyporus betulinus*. In the nursery some dying Scots pines were accounted for by the finding of rhizomorphs of *Armillaria mellea*. *Ustulina vulgaris* was abundant on standing beeches both in these woods and in Arundel Park. The route followed ended up at the north end of Rewell Wood and Arundel Park, where tea was obtained at Whiteways Lodge.

On Sunday the greater part of the collecting was done amongst parasitic fungi in various gardens in Arundel. In the morning some of the members explored the large kitchen garden and the flower garden of the Norfolk Hotel, and secured a number of species of interest to plant pathologists. *Uromyces Betae* and *Ramularia beticola* were found to be abundant on old leaves of Spinach Beet, while a heap of old cabbage stumps provided material of *Gibberella cyanogena*. Among diseases which do not find a place in the following list were noted Reversion in black currants and *Bacterium Delphinii* on larkspurs.

On Sunday afternoon, by kind permission of Her Grace the Duchess of Norfolk, the party was conducted over the gardens of Arundel Castle by the estate agent, Mr G. F. Drake. Near the entrance gate was noted a plane tree badly attacked by *Gnomonia veneta*, and a lime with leaves spotted by *Gloeosporium Tiliae* var. *maculicola*. Later on *Phomopsis Sophorae* was

* This fungus was unfortunately redescribed by Bresadola (Ann. Myc. XVIII (1920), 48), under the name of *Gloeocystidium croceotingens*, with an incorrect citation of the present author (who had sent him specimens) as authority. The fungus is an undoubted *Bourdotia*, but belongs, as Bourdot has pointed out, to the series of *Gloeocystidium caesiocinereum*, *Sebacina cinerea*, etc.

obtained from dead twigs of a fine *Sophora japonica*, and *Diplodia laurina* Sacc. from dead twigs of *Laurus nobilis*. The latter fungus appears to be a new record for this country. In the kitchen garden the most interesting find was *Sclerotinia Mespili* on medlar, the attack being very noticeable on account of the browned leaves, and the curious sweet odour of the conidial stage of the fungus.

On Monday Batworth Park Plantation, lying to the east of the river Arun, was worked. The ground here was fairly damp, and the wood, although small, proved more productive than most of the ground traversed on the Saturday. Ash occurred intermixed with oak, and fallen branches of ash provided such species as *Cryptosphaeria eunomia*, and large specimens of *Daldinia concentrica*. Other finds were *Radulum quercinum*, *Heterochaetella crystallina*, *Tulasnella violea*, and *Cercospora Rubi* Sacc., the last a new record for Britain. At the end of the day the party was entertained at tea by Mr and Mrs J. Fowler of Sefton Place. There a walk round the garden provided a few additional records. In particular the interest of pathologists present was aroused by the finding of abundant material of *Pseudoperonospora Humuli* on hop plants in a hedge.

The meeting concluded with hearty votes of thanks to the Duchess of Norfolk and to her agent Mr Drake for facilities given for working on the estate, and to Mr Fowler for his assistance in general arrangements.

The following list includes all the species which have been determined, and the Secretary is indebted to all the members present for assistance in compilation. The record of *Ligniera Junci* was forwarded by Mr W. R. I. Cook, who found it on roots of some water plants taken by him.

Species marked with an asterisk are new to Britain and will be described.

Complete List of Species gathered during the Foray.

R. = Paine's and Rewell Woods; *A.* = Arundel Castle gardens and other gardens in Arundel; *B.* = Batworth Park Plantation.

HYMENOMYCETES.

Armillaria mellea (Vahl.) Fr., rhizomorphs only, *R.*, *B.*
Laccaria laccata (Scop.) B. & Br., *R.*
Collybia platyphylla (Pers.) Fr., *R.*, leucomyosotis Cooke & Smith, *R.*
Mycena filopes (Bull.) Fr., *B.*
Lactarius pubescens Fr., *R.*
Marasmius peronatus (Bolt.) Fr., *B.*, dryophilus (Bull.) Karst., *R.*
Nolanea proletaria Fr., *R.*, *B.*
Pholiota praecox (Pers.) Fr., *B.*
Galera hypnorum (Schrank) Fr., *R.*, *B.*
Tubaria furfuracea (Pers.) W. G. Smith, *R.*, *B.*
Cortinarius (Hydrocybe) leucopus (Bull.) Fr., *R.*
Stropharia aeruginosa (Curt.) Fr., *B.*

Hypholoma fasciculare (Huds.) Fr., *R.*, *A.*, *B.*, velutinum (Pers.) Fr., *A.*
Psilocybe foenisecii (Pers.) Fr., *R.*
Coprinus atramentarius (Bull.) Fr., *B.*, picaceus (Bull.) Fr., *R.*, micaceus (Bull.) Fr., *R.*, plicatilis (Curt.) Fr., *R.*
Panaeolus sphinctrinus Fr., *R.*, campanulatus (Linn.) Fr., *R.*
Psathyrella disseminata (Pers.) Fr., *B.*
Boletus elegans (Schum.) Fr., *R.*, *B.*
Lenzites betulina (Linn.) Fr., *R.*
Polyporus lentus Berk., *R.*, betulinus (Bull.) Fr., *R.*, squamosus (Huds.) Fr., *B.*, adustus (Willd.) Fr., *A.*
Fomes annosus Fr., *R.*, *B.*, ferruginosus (Schrad.) Massee, *R.*
Ganoderma applanatum (Pers.) Pat., *R.*, *A.*
Polystictus versicolor (Linn.) Fr., *R.*, *B.*
Poria hymenocystis B. & Br., *B.*, obducens (Pers.) Fr., *B.*
Daedalea quercina (Linn.) Fr., *R.*, *B.*
Merulius corium (Pers.) Fr., *R.*
Irpex obliquus (Schrad.) Fr., *R.*, *B.*
Radulum quercinum Fr., *B.*
Odontia farinacea (Pers.) Quél., *B.*
Stereum hirsutum (Willd.) Fr., *R.*, *B.*, purpureum (Pers.) Fr., *R.*, *A.*
Hymenochaete rubiginosa (Dicks.) Lév., *R.*
Corticium laeve (Pers.) Fr., *R.*, *B.*, niveo-cremeum v. Hoehn. & Litsch., *R.*, *B.*, Sambuci (Pers.) Fr., *B.*, botryosum Bres., *R.*, confluens Fr., *R.*, *B.*, confine Bourd. & Galz., *R.*, *B.*, porosum Berk. & Curt., *R.*, praetermissum (Karst.) Bres., *R.*, *B.*
Peniophora pallidula Bres., *R.*, longispora (Pat.) v. Hoehn. & Litsch., *R.*, cremea Bres., *R.*, velutina (DC.) Cooke, *R.*, *B.*, setigera (Fr.) Bres., *R.*, *B.*, hydnoides Cooke & Massee, *R.*, *B.*, cinerea (Fr.) Cooke, *R.*, *B.*, laevigata (Fr.) Massee, *R.*, quercina (Pers.) Cooke, *R.*
Auricularia auricula-Judae (Linn.) Schroet., *B.*, mesenterica (Dicks.) Fr., *B.*
Tremella mesenterica (Retz.) Fr., *B.*
Exidia glandulosa (Bull.) Fr., *B.*, Thuretiana (Lév.) Fr., *R.*, *B.*
Eichleriella spinulosa (Berk. & Curt.) Burt, *R.*
Heterochaetella crystallina Bourd., *B.*
Bourdotia Eyrei Wakef., *R.*
Tulasnella violea (Quél.) Bourd. & Galz., *B.*, *(Gloeotulasnella) cystidiophora v. Hoehn. & Litsch., *R.*

UREDINEAE.

Uromyces Ficariae (Schum.) Lév., *B.*, Fabae (Pers.) de Bary, *B.*, Betae (Pers.) Tul., *A.*, Scillarum (Grev.) Wint., *R.*, *B.*, Dactylidis Otth. (aecidium), *A.*
Puccinia Violae (Schum.) DC., *R.*, Malvacearum Mont., *A.*, Saniculae Grev., *R.*, obtegens (Link) Tul., *A.*, Primulae (DC.) Duby, *B.*, Vincae (DC.) Berk., *A.*, Menthae Pers., *A.*, Buxi DC., *A.*, Caricis (Schum.) Rebent., *A.*, glumarum (Schum.) Eriks., *B.*, Phragmitis (Schum.) Koern. (aecidium), *B.*, Poarum Niels. (aecidium), *A.*
Phragmidium Rubi (Pers.) Wint., *B.*, violaceum (Schultz) Wint., *R.*, *B.*
Pucciniastrum Circaeae (Schum.) Schroet., *B.*, Epilobii (Pers.) Otth., *R.*
Milesina Scolopendrii (Fckl.) Jaap, *A.*
Melampsorella Symphyti (DC.) Bubak, *A.*

USTILAGINEAE.

Entyloma Ranunculi (Bon.) Schroet., *R.*

PYRENOMYCETES.

Podosphaera oxyacanthae (DC.) de Bary, *R.*, leucotricha (E. & E.) Salmon, on apple and pear, *A.*
Erysiphe Polygoni DC., on *Aegopodium*, *A.*, cichoracearum DC., on *Symphytum*, *B.*
Uncinula Aceris Sacc., *B.*

Phyllactinia corylea (Pers.) Karst., on *Cornus*, *B.*
Gibberella cyanogena (Desm.) Sacc., *A.*
Nectria cinnabarina (Tode) Fr., *A.*, galligena Bres., on apple and pear, *A.*, episphaeria (Tode) Fr., *B.*
Hypocrea fungicola Karst., on *Polyporus betulinus*, *R.*
Leptospora spermoides (Hoffm.) Fckl., *B.*
Stigmatea Robertiani Fr., *R.*, *A.*
Mycosphaerella maculiformis (Pers.) Schroet., *R.*, brassicicola (Duby) Lindau, *A.*, Fragariae (Tul.) Lindau (conidia), *A.*, hedericola (Desm.) Lindau, *B.*
Venturia inaequalis Aderh. (conidia only), *A.*, pirina Aderh. (conidia only), *A.*
Leptosphaeria Rusci (Wallr.) Sacc., *R.*, acuta (Moug. & Nestl.) Karst., *R.*, *B.*
Gnomonia veneta (Sacc. & Speg.) Kleb. (conidia), *A.*
Cryptosphaeria eunomia (Fr.) Fckl., *B.*
Diatrypella quercina (Pers.) Nke., *R.*, *B.*
Diatrype Stigma (Hoffm.) de Not., *R.*, *B.*
Hypoxylon coccineum (Bull.) Fr., *R.*, *A.*, *B.*, multiforme Fr., *R.*
Daldinia concentrica (Bolt.) Ces. & de Not., *R.*, *B.*
Ustulina vulgaris Tul., *R.*, *A.*
Xylaria Hypoxylon (Linn.) Grev., *B.*
Phyllachora graminis (Pers.) Fckl., *B.*

HYSTERIACEAE.

Dichaena quercina Fr., *R.*, *B.*
Rhopographus Pteridis (Sow.) Wint., *R.*

DISCOMYCETES.

Aleuria ampliata (Pers.) Gill., *R.*
Peziza aurantia Pers., *B.*
Ciliaria scutellata (Linn.) Quél., *B.*
Coprobia granulata (Bull.) Boud., *B.*
Ascobolus stercorarius (Bull.) Schroet., *B.*
Exoascus deformans (Berk.) Fckl., *A.*
Orbilia xanthostigma Fr., *B.*
Sclerotinia cinerea Schroet., *A.*, Mespili Schell., *A.*
Chlorosplenium aeruginosum (Oeder.) de Not., *R.*, *B.*
Helotium herbarum (Pers.) Fr., *R.*
Dasyscypha virginea (Batsch) Fckl., *R.*, *B.*
Arachnopeziza aurelia (Pers.) Fckl., *R.*, *B.*
Mollisia cinerea (Batsch) Karst., *R.*, *B.*
Pseudopeziza Trifolii (Biv.-Bern) Fckl., *B.*

PHYCOMYCETES.

Cystopus candidus (Pers.) de Bary, *A.*
Plasmopara nivea (Unger) Schroet., *A.*
Bremia Lactucae Regel, *A.*
Peronospora calotheca de Bary, *A.*, parasitica (Pers.) Tul., *A.*, alta Fckl., *A.*
Pseudoperonospora Humuli (Miy. & Tak.) Wilson, *A.*

PROTOMYCETACEAE.

Protomyces macrosporus Ung., *A.*

SPHAEROPSIDACEAE.

Phyllosticta hedericola Dur. & Mont., *R.*, *B.*
Phoma acuta Fckl., *B.*
Phomopsis Sophorae (Trav.) Grove, *A.*, cinerascens Trav., *A.*
Actinonema Rosae (Lib.) Fr., *A.*
Septoria Rubi West., *R.*, Stellariae Rob. & Desm., *A.*, Apii Bri. & Cav., *A.*, Petroselini Desm., *A.*
*Diplodia laurina Sacc., on *Laurus nobilis*, *A.*
Gloeosporium Tiliae Oud. var. maculicola Allesch., *A.*, concentricum Grev., *A.*
Discella strobilina (Desm.) Died., *A.*

HYPHOMYCETES.

Oidium Euonymi-japonicae (Arc.) Sacc., *A.*, alphitoides Griff.& Maubl., *R.*
Ovularia obliqua (Cooke) Oud., *R.*, *A.*, *B.*, Veronicae Fckl., *A.*
Botrytis cinerea Pers., *A.*, Tulipae (Lib.) Hopkins, *A.*
Rhinotrichum repens Preuss, *R.*, Thwaitesii B. & Br., *B.*
Ramularia Primulae Thuem., *R.*, Urticae Ces., *R.*, Taraxaci Karst., *A.*, brunnea Peck, *A.*, beticola Fautr. & Lamb., *A.*
Tilachlidium tomentosum (Schrad.) Lindau, on *Trichia varia*, *B.*
Vermicularia trichella Fr., *B.*
Bispora monilioides Corda, *R.*
Heterosporium gracile Sacc., *A.*
*Cercospora Rubi Sacc., *B.*

MYCETOZOA.

Ligniera Junci (Schwartz) Maire & Tison, *A.*
Lycogala epidendrum Fr., *A.*
Stemonitis fusca Roth., *B.*
Reticularia Lycoperdon Bull., *B.*
Arcyria denudata Wettst., *B.*
Trichia varia Pers., *B.*, Botrytis Pers., *B.*

NOTES ON THE CANKER FUNGUS (NECTRIA GALLIGENA BRES.).

By W. A. R. Dillon Weston, M.A.,

School of Agriculture, Cambridge.

(With Plates I–III.)

I. Shrivelled "Worcester Pearmain" Apples bearing Perithecia of *Nectria galligena*.

The occurrence of perithecia on "mummied" apples. During March, 1925, in an orchard of Worcester Pearmain apple trees, a shrivelled apple was found bearing the perithecia of *Nectria galligena*.

The trees were moderately attacked by "canker." Spurs and leaders showed both the *Fusarium* and perithecial stages.

In order to ascertain the prevalence of this fungus on the shrivelled fruits, seven hundred were collected from the trees and examined. Three apples only were found to be bearing perithecia (see Plate I, fig. 1): and in these the ascospores were mature.

Fungal flora of the fruits. Three hundred and seven apples were kept in a moist chamber for a few days and then the fungus most in evidence upon each was noted, as in Table I.

Table I.

Fungus	No. of apples showing the fungus
Nectria galligena (conidial stage—*Fusarium Willkommii**)	15
Fusarium sp.	42
Diaporthe perniciosa	96
Cytospora sp.	46
Botrytis sp.	14
Penicillium sp.	5
Venturia inaequalis	53
Monilia fructigena	36

Development of perithecia on apples kept under moist conditions. The shrivelled apples collected on March 26th were kept under moist conditions in large crystallising dishes until May 22nd. They were examined at various intervals to observe if perithecia had formed.

Observations are summarised in Table II.

Table II.

Date of observation	Apples showing perithecia	Remarks
April 20th ...	8	On some apples only one or two isolated perithecia were formed.
April 25th ...	2	
May 4th ...	0	
May 15th ...	10	The majority were immature
May 22nd ...	0	

Percentage of fruits with perithecia. Of the remaining seven hundred apples kept under the same conditions, twenty-six developed perithecia, so that, of the total number, forty-nine (or 7 per cent.) are presumed to have been infected with the "canker" fungus.

On March 10th, 1926, two hundred shrivelled apples were collected from the same orchard, and on two of these the perithecia of *Nectria galligena* were found.

In order to obtain some clue to account for the presence of perithecia upon shrivelled fruits, two series of experiments were conducted during 1925.

(1) Twenty-five shrivelled apples were collected from clean spurs.

(2) Twenty-five shrivelled apples were collected from "cankered" spurs.

Table III.

(i) *Apples from clean spurs.*

Date	April 25th	May 12th	May 15th	May 22nd	Remarks
No. of apples showing perithecia	0	0	0	7	Two apples shortly after being moistened showed the *Fusarium* stage

* *Fusarium Willkommii* Lindau = *Cylindrocarpon Mali* (Allesch.) Wollenw.

(ii) *Apples from "cankered" spurs.*

Date	April 25th	May 12th	May 15th	May 22nd	Remarks
No. of apples showing perithecia	0	4	11	14	Twenty-one apples shortly after being moistened showed the *Fusarium* stage

A possible explanation is that in series (ii) the mycelium had worked upwards through the spur and petiole to the shrivelled fruit and had there sporulated, eventually to produce the perithecial stage of the fungus.

In series (i) some free conidia may have been resting upon these apples and later on developed and fructified.

There is, however, a third possibility, viz. that the apple itself was at an earlier date infected with the "canker" fungus, that the apple rotted on the tree, and that when left in the laboratory under more advantageous conditions than would exist in the field, the final stage of the fungus was then produced. This presumes an apple rot occasioned by either (1) infection of the fruit with the conidial stage of apple canker (*Fusarium Willkommii* Lindau), or (2) infection of the fruit with ascospores of *Nectria galligena* Bres.

Inoculations. A seedling apple tree was inoculated during March, 1925, in three places, with ascospores obtained from the perithecia found occurring upon these shrivelled fruits. In November of the same year canker lesions were evident, but at the present date the growth of the fungus in the branch has been arrested. Inoculations were carried out by placing spores in drops of distilled water and introducing them to a small vertical cut in the bark.

II. An "Eye Rot" of Worcester Pearmain Apples caused by the Conidial Stage of *Nectria galligena* Bres.

Occurrence in Cambridgeshire. On July 7th, 1925, five hundred recently fallen Worcester Pearmain apples from this same Cambridgeshire orchard were collected and one was found to be rotting at the "eye." These were kept in the laboratory under dry conditions and examined three weeks later, when four of them showed a similar "eye rot."

At later dates, July 27th and 30th, five other apples were found similarly affected in this orchard; and subsequently many others were obtained.

Wisbech, Isle of Ely. Visits were made on August 6th and 12th to an orchard of Worcester Pearmains near Wisbech, and this disease was very evident on the fruits.

Both orchards are subject to "canker": very few old and deep-seated cankers are present, but girdling of first year wood, and lesions upon fruit spurs are very common.

An "eye rot" of pears* similar to the "eye rot" of apples has also been observed in this area, but has not been fully investigated. (See Section IV.)

Symptoms of this Disease. Diseased fruits ripen and colour prematurely, and are also characteristic in that the rot first starts at the calyx end.

The top of the apple then becomes slightly flattened, becoming more so as the disease progresses.

The skin and flesh of affected fruits are brown, but of a darker brown than rotting produced by *Penicillium* sp. Small raised pustules of the conidial stage (*Fusarium Willkommii* Lindau) of the canker fungus appear; these are of a dirty white colour, sometimes with a tinge of pink (see Plate I, fig. 2).

Distribution. Professor E. S. Salmon and Dr H. Wormald, Wye College, Kent, have recorded in the *Wye Journal* an apparently similar "eye rot" of Worcester Pearmain Apples. Their photographs of this disease are comparable with our own and it would appear that the two diseases are identical.

Their description of this disease is as follows:

"The diseased areas on the young apples obtained from Sussex in July bore closely aggregated pustules with very numerous conidia. The conidia are cylindrical, with rounded ends, usually slightly curved, and septate.

"The septa in the great majority of cases are 3–5 in number the 5-septate conidia being of very frequent occurrence.

"The dimensions vary considerably, the average size being about $50 \times 6\,\mu$, but conidia measuring from $25 \times 5\,\mu$ to $70 \times 7\,\mu$ were met with."

These conidia in size, shape and septation resemble those of the *Fusarium* which is the "summer stage" of *Nectria galligena*, the fungus producing "canker" in apple trees.

The second reference brought to my notice by Dr G. Pethybridge is: Ferdinandsen, C., "Ueber einen Angriff von Krebs

* Since this was written the "eye rot" of pears has been more fully investigated and Dr Wollenweber has confirmed the suggestion that the disease is due to *Cylindrocarpon Mali* (Allescher) Wr., stating, *in litt.*:

"It is interesting to note that in Denmark the apple variety 'Signe Tillisch,' in Baarn, Holland, the 'Present of England' apple and in England the 'Fertility' pear and probably a few other pear and apple varieties are some exceptions to the rule that the canker organism *Nectria galligena* usually does not rot the fruit. In German varieties of apple and pear the *Nectria* fruit-rot does not seem to occur to any extent, although my first finding of its conidial stage was in the endocarp of an apple at Dahlem, as published in *Grundlagen*, 1910, p. 174, under *Fusarium Willkommii* Lindau, and in *Phytopathology*, 1913, p. 226, under *Cyl. Mali* (All.) Wr."

A note appeared on this in the *Gardener's Chronicle* for Nov. 6th, 1926.

(*Fusarium Willkommii* Lind.) an Apfel und Birnfrüchten," *Angewandte Bot.* IV (1922), 173–184. It is there recorded that in Denmark in the autumn of 1919 a new disease of ripening apple and pear fruits appeared with which the conidial stage of *Nectria galligena* was associated: also that this disease of the fruits was capable of causing cankers on the twigs.

Experimental. Twelve Worcester Pearmain apples were inoculated with conidia of this fungus, and were kept in a large crystallising dish. After three to four days brown areas were apparent at the point of inoculation. Later the apples flattened out at this point and typical conidial pustules of the fungus appeared (see Plate III, figs. 1 and 2).

Apples found on July 7th were kept under moist conditions. Towards the end of August perithecia developed, but asci were not mature. The apples by then were completely rotten and saprophytic fungi had developed.

On August 7th apple trees in our experimental plot were inoculated with the fungus obtained from "eye rot" apples. Twelve inoculations were made and controls were left.

On August 15th, twelve branches of Worcester Pearmain trees in a different area were inoculated in the same manner. By November 4th typical "canker" lesions were apparent in both series and the conidial stage was reproduced upon them.

Cultures. Cultures were made from diseased fruits, the medium used being apple agar. Typical macro-conidia were formed, the spores being cylindrical, slightly curved, septate, and rounded at the ends.

The spores varied in size, the average being between 40–60 μ × 5–5·5 μ. They were more often four- than five-septate. These measurements were taken from a culture three and a half months old.

Spore measurements from twigs artificially cankered, by infection with spores from "eye rot" apples, were generally between 56–70 μ × 5–6 μ, and five-septate. After three and a half months perithecia had not developed in culture but the mycelium had compacted into brownish red tufts.

Intensity of the disease. This was studied in an orchard of Worcester Pearmains in which we had carried out a series of spray trials to check "scab."* In these experiments the fruit was graded by hand. The first picking of fruit took place on August 20th, the second on August 25th, the main bulk being pulled on September 10th.

During the first picking, the fruit showing "eye rot" was weighed separately. The results obtained in these various plots are tabulated in Table IV.

* Journ. Min. of Agric. March, 1926.

For the first spraying lime sulphur was used at the strength of 1 in 30 and for the second spraying at 1 in 60. Where lead arsenate was added this was at the rate of 2 lb. of arsenate of lead paste to 40 gallons. The first spraying was carried out on May 13th, the second on June 3rd.

These figures are interesting in that they show that the spraying methods adopted to control apple "scab" were also effective in reducing "eye rot."

It should be noted, however, that these figures have no bearing upon the actual weight of fruit showing "eye rot" in this orchard. On the two subsequent pickings the disease was much less.

Table IV.

Row	Spray	Weight of clean fruit	Weight of fruit showing "eye rot"	% of "eye rot" to nearest whole number
		lbs.	lbs.	
2/3	Lime sulphur plus lead arsenate (twice)	31¾	2½	8
4/5	Ditto (once)	40½	6	15
6	Control	24	9¾	41
7/8	Normal Bordeaux (8 : 8 : 100) plus lead arsenate (twice)	4	0	0
13/14	Ditto (once)	25½	5½	22
15	Control	30	16½	55
16/17	Ex. Bordeaux (25 : 8 : 100) plus lead arsenate (twice)	14¾	2¼	15
18/19	Ditto (once)	15	1½	10
20/21	Prop. Bordeaux lead arsenate (twice)	13¾	2¾	20

The reason why greater weight of diseased fruit was obtained in this first picking is accounted for by the fact that the pickers pulled what they considered the more mature fruit. This was deceptive, because, in this variety a characteristic symptom is apparent earlier maturity and deep colouring.

III. The Wilting of Worcester Pearmain Blossom Trusses.

When the Worcester Pearmain trees in the above orchard were in flower, it was noticed that a few trusses on each tree were wilting.

On June 10th, twenty-five of these spurs were labelled and examined at intervals, and on July 30th, seventeen of them were showing "canker" lesions.

Twenty-five of these twigs were also washed with distilled water, each placed in a boiling tube, plugged with cotton wool, and kept until August 20th.

Five then showed the conidial stage of "canker," and two others had developed perithecia, the asci in one being mature, the asci in the other immature.

This evidence points to the "canker" fungus as being the cause of the wilting of these trusses, but no explanation is advanced as to the mode of infection.

IV. Notes on Pear Canker.

An "eye rot" of pears similar to the "eye rot" of apples was observed in an orchard at Wisbech: and during March, 1925, a shrivelled pear with a few scattered perithecia was found still adhering to the tree in an orchard in that area.

While visiting a large commercial plantation near Cambridge in April, 1926, an unusual form of pear canker was observed. The fruit trusses were found to be wilting and many were discoloured, the fruit stalks being black at the base. Leaves attached to these trusses were also discoloured, being black or blackish brown; diseased areas were noted at the base and middle of the petioles. Spores similar to the *Fusarium* stage of *Nectria galligena* were obtained from some of the leaf and fruit stalks. Lesions were observed on the young shoots of the previous year's growth, and these bore pustules typical of *Nectria galligena*. Pitmaston Duchess trusses were also found similarly affected at Bluntisham in Hunts. R. V. Harris* has described a somewhat similar form of canker on a trained pear tree (var. Beurré Diel) in a private garden at West Malling, but no mention was made of withering of fruit trusses, leaf symptoms only being described.

Mode of Infection. Wiltshire† has described infection through leaf scars and scab lesions; and Harris* infection of the current year's shoots through the bases of leaves still upon the tree. In this latter case it was not ascertained whether previous infection by the scab fungus was necessary for the canker fungus to gain an entrance. It is of interest therefore to state that these leaves similarly attacked, showed no scab fungus, nor had it at that date been observed on either pear or apple.

A further investigation is being made, to ascertain if the infection is stigmatic.

* Harris, R. V. An Unusual form of Pear Canker. Ann. Rep. East Malling Res. Stat. 1924.

† Wiltshire, S. P. Studies on the Apple Canker Fungus. I. Leaf Scar Infections. Ann. App. Biol. VIII. II. Canker Infections of Apple Trees through Scab Wounds. Ibid. IX.

SUMMARY.

1. One method of over-wintering of the apple "canker" fungus (*Nectria galligena* Bres.) is by the formation of perithecia upon shrivelled fruits.

2. The *Fusarium* stage of "canker" (*Fusarium Willkommii* Lindau) is responsible for an "eye rot" of Worcester Pearmain.

3. Evidence is brought forward to show that one case of wilting of Worcester Pearmain blossom trusses was due to the canker fungus, but no explanation is advanced as to the mode of infection.

4. An unusual form of pear canker is described.

In conclusion, I wish to thank Miss E. M. Wakefield, and Mr F. T. Brooks, for confirming the identification of the conidial stage of *Nectria galligena* Bres. upon the "eye rot" apples, and Messrs F. T. Brooks and F. R. Petherbridge for helpful criticism.

EXPLANATION OF PLATES I–III.

PLATE I.

Fig. 1. Shrivelled Worcester Pearmain apple surface covered with perithecia of *Nectria galligena*. $\times 4\frac{1}{2}$.

Fig. 2. Four Worcester Pearmain apples showing typical "eye rot." Nat. size.

PLATE II.

Twig of Worcester Pearmain showing apple with "eye rot." Nat. size.

PLATE III.

Fig. 1. "Eye rot" obtained from Wisbech orchard. Reduced $\frac{1}{2}$.

Fig. 2. "Eye rot" produced in healthy apples (var. Worcester Pearmain). By inoculation of conidial spores of "canker." Reduced $\frac{1}{2}$.

THE DEVELOPMENT OF GEASTER VELUTINUS.

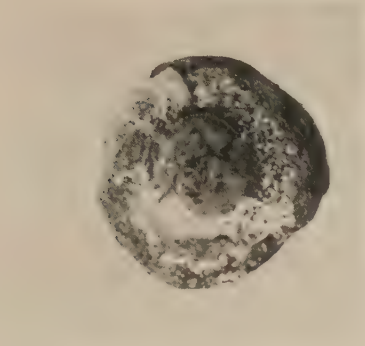
By G. H. Cunningham,

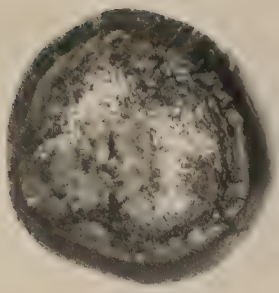
Government Mycologist, Biological Laboratory, Wellington, N.Z.

(With 9 Text-figs.)

So far as I am aware no study of the development of any species of the genus *Geaster*, nor of the related genera *Astraeus* and *Myriostoma* has been undertaken previously.

With a view to working out its development the writer searched for and obtained some twelve developmental stages of the epigaean species *Geaster velutinus* Morg., one of the commonest species of the genus present in New Zealand. These young plants were growing in the vicinity of numerous mature plants in a locality in the forest where the species has, to the writer's knowledge, been present for the past six years. It produces a superficial mycelial subiculum—quite noticeable in some cases, scarcely discernible in others—and upon this the young plants were found.





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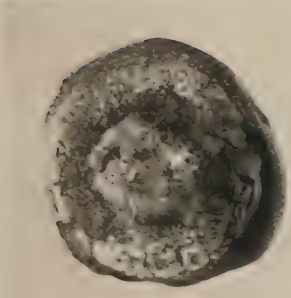

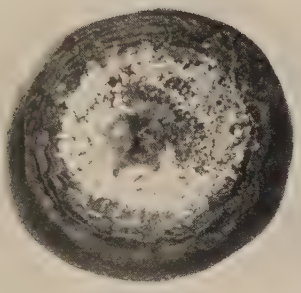

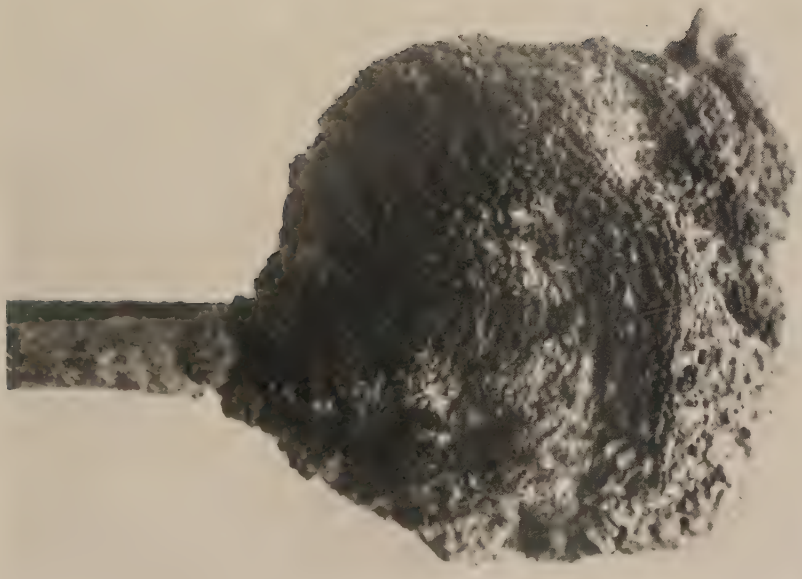

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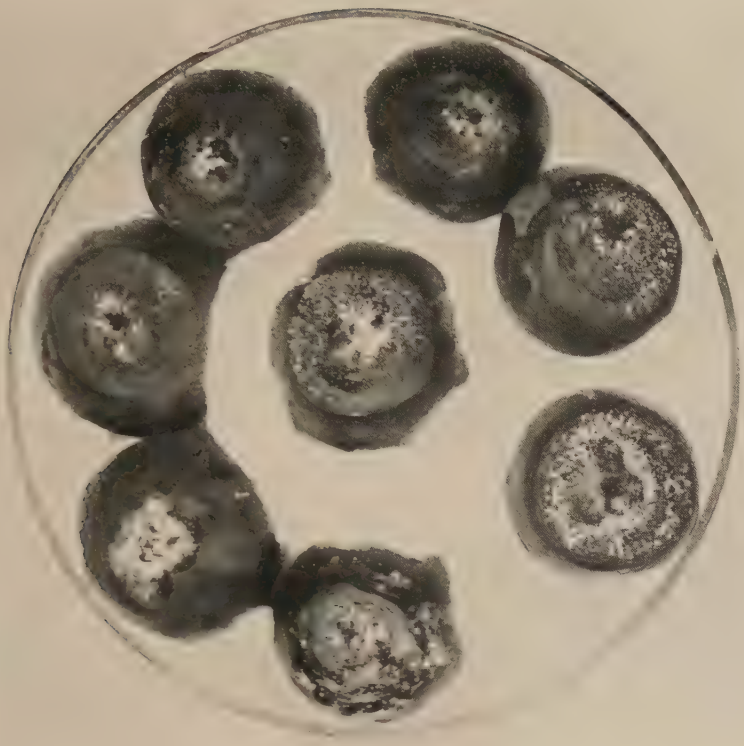

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Specimens were fixed in picro-formol, embedded and sections 5 μ and 10 μ were cut with a rotary microtome. These were stained with iron-alum haematoxylin and light green, and mounted in canada balsam.

Structure of the Mature Plant.

A typical specimen immediately before expansion is globose or ovate, superficial, 2–3 cm. diam., and attached at the base to the mycelial subiculum by a strongly developed mycelial cord. If sectioned the plant is seen to consist of several exterior layers enclosing a central sac. The outer layers subsequently split from the apex downwards into several stellate rays which remain expanded and appressed to the substratum or else become revolute, lifting the plant clear from it. The expanded

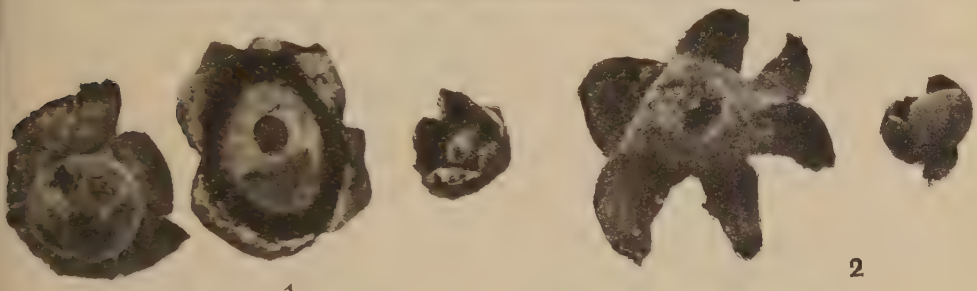

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Fig. 1. *Geaster velutinus* Morg. × ⅔. Saccate specimen in the centre, revolute specimen on the left, expanding plant on the right.
Fig. 2. Exterior of the exoperidium showing the tomentose exterior (more noticeable on developing plant on the right) and prominent umbilical scar—the point of attachment. × ⅔.

plant now has a stellate but somewhat saccate appearance (Fig. 1), and bears in the centre a spore sac which is thin, membranous and perforated apically by a single opening, outlined by a more or less silky or fibrillose zone.

Thus the expanded plant is seen to consist of two well-defined groups of tissues, the stellate part being the exoperidium, the spore sac the endoperidium.

Exoperidium.

The exoperidium consists of three well-defined tissues:

(1) the mycelial or outer layer;
(2) the fibrillose or middle layer; and
(3) the fleshy or inner layer.

(1) *Mycelial layer.* This, the exterior layer, is well seen in unexpanded plants, being in the nature of a dense palisade, 1–2 mm. or more thick, of stout, deeply coloured, persistent hyphae. This layer persists throughout the lifetime of the plant,

and is, in fact, the principal character by which the species is distinguished from several related epigaean species.

(2) *Fibrillose layer.* This consists of intricately woven hyphae of two kinds, arranged with their long axes predominantly radial. The inner portion, next to the fleshy layer, is strengthened by numerous thick-walled hyphae similar to those of the capillitium. The whole tissue is tough and cartilaginous.

(3) *Fleshy layer.* This is pseudoparenchymatous. In freshly expanded plants it is soft, thick and flesh-coloured; after exposure it shrinks considerably, changes to some shade of brown, and often becomes rimose.

Endoperidium.

This structure encloses the gleba, consisting of capillitium and spores, and is attached by a broad base to and partially enclosed by the saccate portion of the exoperidium (Fig. 1). In texture it is membranous, and consists of numerous interwoven, partially gelatinised hyphae.

At the apex is a solitary stoma through which the spores escape. In this species the stoma is surrounded by a zone of parallel fibrils arranged radially, forming a broad, depressed zone.

The spores are globose, dark fuscous brown, strongly verrucose and reticulate, and very small, being 4–4·5 μ diameter.

The capillitium consists of innumerable fusiform, deeply-coloured, simple, continuous hyphae.

Outline of Development.

Development proceeds in the following order:

(1) Differentiation of the mycelial layer of the exoperidium.

(2) Simultaneous differentiation of the fleshy and fibrillose layers, gleba and columella.

(3) Lacunae appear in the gleba, and become lined with a palisade of primary basidia.

(4) Extension of development of lacunae with accompanying palisade of basidia, together with the formation of tramal plates, and later with the appearance of secondary basidia. This is the stage of intense spore production.

(5) The endoperidium becomes differentiated.

(6) Glebal formation (excluding the formation of the capillitium) is concluded.

(7) Peristome and stoma are formed.

(8) Tramal plates of the gleba become broken down and fragmented, and the capillitium grows out from the columella and endoperidium.

(9) The exoperidium becomes revolute and exposes the endoperidium.

Plants are first noticeable when about 2 mm. diam. At this stage they are composed of hyphae of two kinds, macro-hyphae 5–7 μ diam., and micro-hyphae 2–3 μ diam. Both are septate, much branched and intricately interwoven. Tissue differentiation begins shortly after plants attain to this size.

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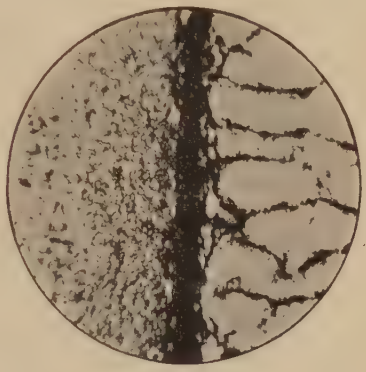

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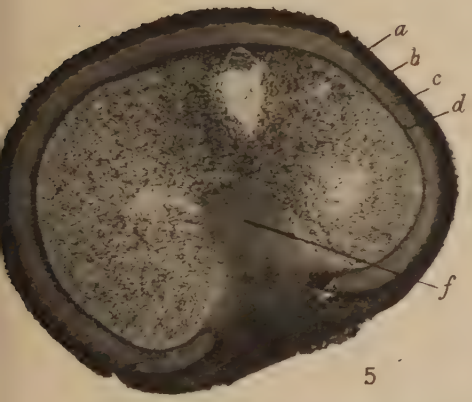

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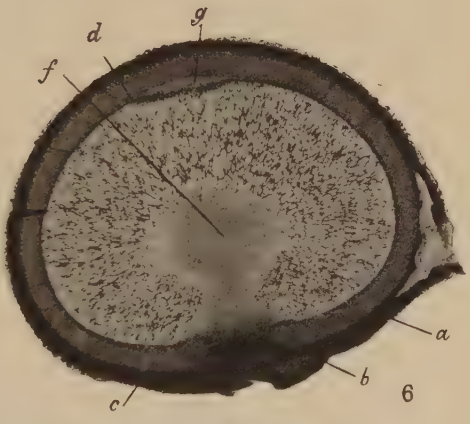

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Fig. 3. Plant showing commencement of differentiation of the gleba and mycelial layer. × 15.

Fig. 4. Later stage showing (*a*) mycelial layer, (*b*) fibrillose layer, (*c*) fleshy layer, (*d*) primordium of the endoperidium, (*e*) glebal mass with lacunae. Section not median. × 10.

Fig. 5. Plant at a later stage; lettering as in the preceding figure, (*f*) columella. Section not quite median. Perforation in the upper portion of the gleba due to insect larva. × 7.

Fig. 6. Median section through plant shortly before collapse of the tramal plates; lettering as above, (*g*) disc of forming peristome. Note that fleshy layer merges abruptly into columella. Wrinkles in fleshy layer formed while section was being affixed to the slide. × 3.

Fig. 7. Photomicrograph of portion of the fleshy layer with the contiguous endoperidium. × 200.

Differentiation of the mycelial layer. In this species a true mycelial layer (as applied to hypogaean species) is wanting, modified hyphae taking its place, forming a tissue which is the first to be differentiated. When plants are approximately 3 mm. diam., numerous dark-walled, unbranched, simple hyphae arise at the periphery directly from the macro-hyphae. They grow radiately from the periphery of the embryonic plant, giving to it a tomentose appearance. As growth proceeds they become elongated, much convoluted, thick-walled, and form a dense layer 1–2 mm. thick, over the exterior (Fig. 4, *a*).

Differentiation of the fibrillose layer. This is first noticeable as a zone of unaltered tissue lying between the mycelial and fleshy layers (Fig. 4, *b*), differentiation beginning about the time the fleshy layer becomes definitely pseudoparenchymatous. At first it consists of both macro- and micro-hyphae, but soon the latter predominate, and become arranged with their long axes radial. Then a third type of hypha makes its appearance, being of the same nature as those forming the mycelial layer, here assuming a position parallel with the latter and serving to strengthen the whole tissue.

The fibrillose layer is of the same nature as primordial tissue (save that micro-hyphae predominate), the fleshy and mycelial layers arising from it as groups of specialised tissues.

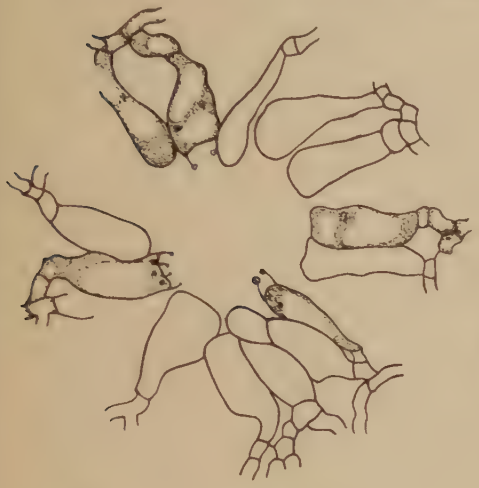
Differentiation of the fleshy layer. Shortly after differentiation of the mycelial layer, the fleshy layer originates as a zone of more closely interwoven and compacted hyphae lying between it and the central region of the plant (primordium of the gleba). This tissue consists almost entirely of macro-hyphae. Soon the hyphal walls become partly gelatinised and the whole becomes pseudoparenchymatous, and is then sharply delimited from the tissues which it encloses and those lying to the exterior (Fig. 4, *c*). It does not form a continuous zone, being interrupted by the thickened base of the columella, into which it abruptly merges (Fig. 6, *c*).

Endoperidium.

This comprises all tissues lying within the fleshy layer, and consists of the spore sac with its contents. In systematic papers it is usual to confine the term endoperidium to the spore sac alone, the capillitium and spores collectively being termed the gleba. This practice will be followed herein.

Gleba. At first this consists of undifferentiated primordium (Fig. 3), but shortly after differentiation of the fleshy layer begins, a dome of lacunae appears between the fleshy layer and the centre of the glebal mass (Fig. 4, *c*), and partially surrounding a non-lacunate region—the columella. The lacunae

arise as simple cavities in the glebal tissue. They vary in size and shape and appear to be formed by the tearing apart of the hyphae. They soon become lined with inflated cells of a size much greater than those of the surrounding hyphae. These inflated cells are in reality basidia, but as they differ greatly from those produced at a later stage they will be termed primary



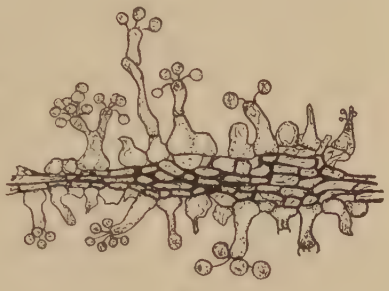


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Fig. 8. Primary basidia. Camera lucida drawing showing the arrangement of basidia around a lacuna in a section 5μ thick. Monosporous basidium in lower figure. × 500.

Fig. 9. Secondary basidia. Camera lucida drawing of portion of a tramal plate showing the gelatinised tissue of the plate (in black), basidia, sterigmata and spores. × 800.

basidia (Fig. 8). Owing to enlargement they compress the intervening tissues (between lacunae) thus giving rise to plates of tissue termed tramal plates (Fig. 6).

The primary basidia are irregular in size and shape and form a close palisade or hymenium lining the lacunae. They arise directly from modified portions of the hyphae of the tramal plates, a sub-hymenium, characteristic of most members of the

Agaricales, being absent. Many become monosporous shortly after their formation (Fig. 8), a condition not uncommon in certain other Gasteromycetes at an early stage in their development. Soon, however, the primary basidia become more regular in shape and bear several spores (usually four at this stage) on short sterigmata.

Next follows a period of rapid formation of lacunae and production of basidia, until the whole of the tissue enclosed within the fleshy layer (or rather the endoperidium, which appears shortly before this active period begins), save the columella, becomes converted into partly gelatinised tramal plates and basidia (Fig. 6).

Basidial development continues rapidly. Each basidium as it matures produces four to eight spores; these become detached, and the basidium collapses, to be replaced by another arising from a hypha of the tramal plate. Owing to this rapid development of basidia the plates become thinner and more lamellar, a change accompanied by a decrease in the size of the basidia. Decrease in size is rapid, so that shortly after spore production has begun the basidia are seen to be less than one-fourth the dimensions of the primary basidia. The smaller ones, which are responsible for the greatest spore production, are here termed secondary basidia (Fig. 9). They are usually four-spored, but eight-spored forms are not uncommon.

This period of intense spore production continues until finally little remains of the tramal plates but strands of partially gelatinised hyphae, with a few adhering, partially collapsed secondary basidia. Then the plates become fragmented and disappear, and at the same time the capillitium threads—hyphae of the same type as those comprising the mycelial layer—make their appearance. These arise principally from the columella; and in lesser numbers from the inner surface of the endoperidium. In consequence the columella becomes smaller as development of the capillitium threads continues, until in the mature plant often scarcely more than a rudiment remains.

The capillitium threads are long, unbranched (save occasionally at the apices), dark in colour, thick walled and acuminately pointed. Thus at maturity the tramal plates have disappeared, the whole of the interior being occupied by the capillitium and spores.

Spore production begins when the plants are 7–8 mm. in diameter, and continues uninterruptedly until the tramal plates break up.

The endoperidium consists of micro-hyphae identical with those of the fibrillose layer. The hyphae become closely and intricately interwoven and partly gelatinised; at first they are

attached both to the tramal plates on the interior and to the fleshy layer on the exterior, but shortly after the endoperidium is clearly defined, partial separation is affected by the tearing apart of the hyphae from the fleshy layer (Fig. 7). When the exoperidium becomes revolute, separation occurs along the junction of the fleshy layer and endoperidium, particles of hyphae persisting for some time as a pruinose covering on both the interior of the one and the exterior of the other.

Peristome. Shortly after the endoperidium has been formed, formation of the peristome begins. The hyphae at the apex of the endoperidium become more loosely interwoven and form a thickened apical disc (Fig. 6, *g*). The hyphae of the disc then assume a radial arrangement, a small irregular cavity appears in the centre and becomes lined with hyphae from the inner portion of the endoperidium. Then the disc collapses, becomes depressed and gives rise to the peristome, which now appears as a circular depressed region perforated by a circular orifice—the stoma (Fig. 1).

Finally rupture of the exoperidium occurs, and the endoperidium is exposed.

Cytology.

The cytology of this species is apparently simple. The hyphae are uninucleate and the nuclei exceedingly small, ranging in size from 0·5 to 1·0 μ in diameter. They are usually found in the vicinity of the septa. The basidia—both primary and secondary —also are uninucleate, the nuclei being about the same size as those of the hyphae. Owing to the exceedingly small size of the nuclei, no chromosomes have been observed.

The behaviour of the nucleus within the basidium during spore production is apparently similar to that of certain other uninucleate Basidiomycetes, the plant appearing to be haploid throughout. The fusion nucleus present in the basidia of *Secotium* and certain species of the Agaricales prior to spore production has not been observed, for at all stages of its development prior to spore production the basidium is uninucleate.

Shortly after the basidium is formed sterigmata grow from the apex. When these are about 3 μ long terminal inflations appear—the developing spores. Until this period the nucleus remains unchanged, but with the beginning of spore formation it rapidly changes, and divides until the number of nuclei are equal to the number of spores produced. Such division may occur in any part of the basidium, but as the sterigmata are developing the nucleus usually takes up a position near the apex of the basidium and there divides. Four is the usual number of spores produced, consequently it is usual to find

this number of nuclei formed by successive divisions of the nucleus. Actual migration has not been observed, owing, no doubt, to the exceeding fineness of the sterigmata (0·25 μ or less) but spores of a diameter of less than 2 μ are seen to possess no nuclei whereas others larger than this are invariably and constantly uninucleate.

At an early stage of development the epispore is quite smooth, but shortly after migration of the nucleus it becomes minutely roughened, and as the spores enlarge the degree of roughness increases until at maturity they are seen to be closely covered with fine, flat-topped verrucae. Immediately after its detachment from the basidium the spore is seen to be shortly pedicellate—due to the persistence of a portion of the sterigma, but this structure apparently disappears, for in spores from a mature plant it is not noticeable.

As all attempts to germinate spores have failed, it has not been possible to observe nuclear behaviour during germination, nor to ascertain whether the first hyphae produced are uninucleate. This peculiarity of non-germination under all laboratory conditions is apparently common in the Lycoperdaceae, for the writer has failed in all attempts to germinate spores of *Bovista*, *Bovistella*, *Calvatia*, *Disciseda*, *Geaster* and *Lycoperdon*. No clamp connections have been observed, either in the vegetative mycelium or in the mycelium of the tissues of the fructification.

All photographs by H. Drake; drawings and photomicrograph by the writer.

NOTES ON NECTRIA RUBI.

I.

By G. H. Pethybridge,

Pathological Laboratory, Ministry of Agriculture and Fisheries, Harpenden.

The diseases of raspberries have not hitherto been the subject of extended investigations in this country. In recent years, however, their importance has become increasingly recognised both by growers and by plant pathologists, and these diseases are now being studied in detail at the East Malling Fruit Research Station* and elsewhere.

* An interesting account of the Verticillium Wilt of Raspberry has already been published by Mr R. V. Harris of this Station (see Journ. Pomology and Hort. Sci. IV (1925), p. 221), and Messrs N. H. Grubb and A. M. Massee have published a short note on Raspberry Mosaic (see Ann. Rept. E. Malling Research Station for 1923, p. 131). *Plectodiscella veneta* Burk., the cause of Raspberry Anthracnose in America, has also recently been identified on English material at E. Malling.

For this reason, and because a number of enquiries have been received on the matter, it seems desirable to put on record a note of some work done a few years ago in Ireland by Mr H. A. Lafferty and myself in connection with a fungus which we regarded as identical with *Nectria Rubi* Osterw.

In the summer of 1916 some dead and dying raspberry plants were received from Sir F. W. Moore, Keeper of the Royal Botanic Gardens, Glasnevin, Dublin. Some of the material came from Co. Dublin and some from Co. Down. On the canes there were certain bleached areas on which perithecia of *Didymella applanata* Sacc. were present, but it was clear that this was not the real cause of the generally unhealthy condition of the plants. After carefully washing away the soil which adhered to the stools, numerous perithecia of what appeared to be a species of *Nectria* were discovered on the crown, close to the points of origin of the canes. Similar perithecia were also found on the bases of canes which had previously been cut back, as well as on the bases of the dead and dying canes still present. The roots were dying or dead, but no perithecia were found on them.

The young perithecia were of a bright red colour, the older ones somewhat darker, while the oldest were almost black. They were more or less spherical, but possessed a short papilla-like neck with an ostiole. Their transverse diameter varied from 300 to 500 μ and the average of several measurements was 450 μ. They were smooth and seated in groups on a stroma which broke out through the bark. In each perithecium there were numerous asci, averaging 120 μ long and 6 μ broad, each containing eight two-celled ascospores arranged in a single row. These spores were slightly constricted in the middle, the two cells being sometimes equal in size, sometimes unequal. They were hyaline, or of a faintly smoky colour, and measured on the average 12·8 × 5·5 μ. When quite ripe their walls were sometimes faintly spinulose. Paraphyses were present and were elongated, thin and whip-like. In ripe perithecia they were seen with difficulty or not at all. When the material was kept for a day or so in a covered moist dish the ascospores were extruded, and lay as a white mass around the ostiole.

When the decaying roots were kept moist, patches of greyish white aerial mycelium developed on them in a couple of days, which microscopical examination showed to belong to a *Fusarium*. The conidia present were 0–5-septate, sickle-shaped, and possessed a distinct "heel"* at the base, where the wall

* For the mode of origin of this "heel" in *Fusarium* conidia see Sci. Proc. Roy. Dublin Soc. xv (N.S.), (1917), 204. The same thing occurs in *Hypomyces Solani*; see Trans. Brit. Myc. Soc. vi (1919), 113. In cultures in which conidia are produced rapidly the "heel" is frequently absent, and it is therefore of little use for diagnostic purposes.

was thinner. They averaged 12 × 5·3 μ when non-septate and 60 × 7 μ when 5-septate; those having from one to four septa were of intermediate sizes between these two extremes. The conidiophores on which they were borne were considerably branched.

On account of the general appearance of the fungus and of its behaviour when grown subsequently in pure culture and in spite of certain slight variations in spore measurements, it was considered to be identical with *Nectria Rubi* described by Osterwalder* in 1911, and was recorded under this name†.

Osterwalder found violet-coloured sporodochia of a *Fusarium* on the roots of diseased raspberry plants. A few days after the material had been placed in a moist dish, perithecia—at first yellowish green and then red—began to develop on the sporodochia, which, from their location, he surmised were connected with the *Fusarium*. Pure cultures were raised, starting from a single ascospore and a single conidium respectively, and from their behaviour it was concluded that the *Fusarium* was a stage in the life history of the *Nectria*. Although the *Fusarium* stage was obtained in cultures emanating from an ascospore, no perithecia developed in any of the cultures. The violet coloration appeared in some instances but not in others, its production being dependent, apparently, on the nature of the substratum used.

A fairly extensive series of parallel cultures on various media was carried through by Mr Lafferty working with the Irish material. The starting-point of each series was a single *Nectria* ascospore and a single *Fusarium* conidium respectively. The cultures behaved similarly in every respect and showed that they appertained to one and the same fungus. The *Fusarium* stage developed rapidly in each series, and after the lapse of nearly six months perithecia also developed in cultures derived from both sources. These perithecia were at first whitish, then yellow and finally red. The asci in them were, on the average, slightly shorter than those in the perithecia on the original raspberry material, but the ascospores were approximately of the same size. In this way, therefore, the connection between the *Nectria* and the *Fusarium* stages was proved by growth in pure culture.

The fungus caused the liquefaction of wort gelatine, and the liquid took on a deep claret colour. Claret-coloured granules were also present in the cells of the submerged hyphae. The same colour was developed on oat-extract agar and Quaker Oat agar. Osterwalder found that his fungus caused the liquefaction

* Osterwalder, A. Ueber eine neue auf kranken Himbeerwurzeln vorkommende Nectria und die dazu gehörige Fusarium-Generation. Ber. d. Deut. Bot. Gesell. XXIX (1911), pp. 611–622.

† Royal Dublin Society, Report of the Council for the year 1916, p. 63.

of raspberry-root-decoction gelatine, and in cultures derived from an ascospore a violet coloration appeared. The same coloration appeared in cultures of similar origin on sterilised potato stalks.

The question of the parasitism of *Nectria Rubi* still remains to be settled. Osterwalder carried out but few infection trials, and only with the *Fusarium* conidia. His results were negative, but he surmised that he might have been more successful had ascospores been used as the inoculum. With the Irish material six healthy raspberry plants of three different varieties growing in pots were inoculated in June, 1917, by the present writer, through wounds in the woody stock below ground level, with material taken from a pure culture on Quaker Oat agar derived from a single ascospore; and five plants of the same varieties, wounded but not inoculated, served as controls. The results, however, were purely negative, and, owing to various difficulties, the work had to be discontinued.

The same fungus now appears to have been discovered on ailing raspberry plants both in Scotland* and in England. It is to be hoped that further research will now be possible and that the question as to whether this fungus really causes a disease of raspberries may be satisfactorily cleared up.

II.

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In view of the finding of *Nectria Rubi* in Ireland and in Scotland, it seems desirable to add a brief note on its occurrence in England.

During the last two years the writer has observed numerous cases of a disease of raspberry canes in the west of England which might well be described as "Crown Rot." The diseased plants appear to make normal cane growth during summer and autumn, but this is followed in spring by the failure or partial failure of the bud-break. Leaves may open normally, but wilting quickly takes place and is followed by die-back of the cane. Examination of affected plants shows that the whole or part of the internal tissue in the region of the crown and main root is discoloured and invaded by fungal hyphae. At a sufficiently early stage, a narrow strip on one side of the root and crown frequently remains healthy; and from this a normal sucker may arise. This sucker remains healthy and makes

* Alcock, N. L. A Note on Raspberry Canker (*Nectria Rubi* Osterwalder). Trans. and Proc. Bot. Soc. Edinburgh, xxix (1925), 197.

normal growth while assimilation is active, but becomes invaded at its base by hyphae when growth ceases, thus bringing about in the following spring the symptoms described, when the diseased tissue extends further up into the affected canes. It is observed that the "plug" which is formed at the base of the preceding year's cane in healthy plants, and which normally prevents the entrance of fungi, fails to form in the diseased canes, so that any fungi inhabiting the old canes continue to grow down into the crown.

In May, 1925, specimens of Baumforth's Seedling, showing the general symptoms described above, were received from Worcestershire. In the region of the crown and upper portion of the main root numerous immature bright red perithecia were scattered singly or occurred in groups on the surface of the bark. The contents of the perithecia consisted of thread-like paraphyses and asci, each of the latter containing eight two-celled ascospores. When mature the perithecia turned almost black, and in a moist atmosphere white tendrils of ascospores were extruded through the ostiole. Such perithecia were spherical, with a slightly papillate ostiole, and measured 420–560 μ in transverse diameter. The asci were club-shaped and hyaline and measured 85–100 $\mu \times 6$–8 μ. The two-celled ascospores were hyaline or faintly coloured, and constricted at the septum. Each cell was slightly pointed and contained one oil drop. The spores measured 11·2–14·7 $\mu \times 5$·5–7 μ. The ascospores were slightly smaller than those described by Osterwalder for *Nectria Rubi* (15·9–18·6 $\mu \times 4$·6–5·2 μ) but the measurements agreed closely with those given by Pethybridge above and by Alcock*. Prior to germination there is a slight enlargement of one or both cells of the ascospore, and it is possible that this may account for the slightly larger size found by Osterwalder.

Plates were poured of a suspension of the ascospores in malt extract agar. The resulting individuals were at first white, but in about ten days they took on a deep violet colour and were found to be bearing conidia of the *Fusarium* type. Typical conidia were hyaline, 3–4-septate, curved, with rounded extremities and measured 45–59 $\mu \times 6$–8 μ.

Though sporodochia of the *Fusarium* stage of *Nectria Rubi* were observed by Osterwalder, and by Pethybridge and Lafferty on the roots of diseased raspberry plants, they have not so far been observed on specimens found in England. Isolations from the inner tissues of roots, however, have yielded violet-coloured mycelium which produces conidia identical with those formed in the cultures derived from ascospores.

Pure cultures derived from ascospores and *Fusarium* conidia

* Loc. cit.

have been studied comparatively on various media. Whatever the origin of the culture, on the same medium, no appreciable difference was observed. In culture, the fungus forms a tuft-like mass with a well-marked strigose margin. This marginal portion is made up of radially arranged fasciculate masses of mycelium, which break up at their tips into individual diverging hyphae. This form of growth is more marked on woody media such as apple wood and raspberry root than on agar and potato media.

On malt extract agar growth is compact and cushion-like with strigose margin. The deep violet colour appears within about ten days and is associated with the formation of conidia; the actively growing mycelium on the margin remains white. In older cultures marked zoning appears, with alternating rings of violet and brown, corresponding to abundant conidial formation and sterile hyphae respectively. The violet colour disappears when growth ceases and no further conidia are formed. No perithecia have been found in agar cultures.

On glycerine-potato slice growth is vigorous with exceptionally abundant conidial formation. The characteristic violet colour is apparent in the early stages; the aerial mycelium, however, soon turns a sepia brown colour. Zones of aerial hyphae 4–5 mm. wide alternate with zones consisting of a white, viscid mass of conidia. The whole of the surface of the cotton-wool plug supporting the slice becomes covered with a similar mass of conidia. After about five months perithecia were observed to be forming on the lower surface of the cotton-wool plug. They were at first white, later, red, eventually turning a dark reddish brown. A well-marked subiculum was present at the base of each perithecium.

On ordinary potato slice growth proceeded more slowly, a white, flocculent mycelium, with pale claret-coloured zones being produced.

On raspberry root and apple wood a deep violet colour is evident in some cases and is more persistent in cultures started from mycelium. On such substrata exceptionally vigorous formation of conidia takes place. On the aerial hyphae the conidia are borne on short much-branched hyphae arising at right angles to the main hyphae and give the mycelium a powdery appearance. In general the colour varies from mauve to chrome-orange. In all cases the violet colour is evanescent, turning later to chrome-orange. The conidia are produced later in viscid masses taking the form either of white, mauve or yellow globules or of a yellow viscid film on the surface of the substratum.

In both apple-wood and raspberry-root cultures, after about

eight weeks, large numbers of perithecia were observed to be forming on the aerial mycelium, 2–3 mm. from the surface of the substratum. They were borne on the tips of the whip-like hyphae which diverge from the fasciculate mycelium, and were at first transparent olive green, but later turned black.

Perithecia from these cultures and from the glycerine-potato culture are somewhat smaller than those occurring in nature and measure 350–490 μ in diameter. The ascospores themselves do not differ in size from those which occur in perithecia on the raspberry. In about twelve weeks the perithecia were mature and extruded their ascospores through the ostiole.

When ripe perithecia were placed in a drop of water ascospores were violently expelled from the ostiole in a series of small explosions, the empty asci being forcibly expelled later in the same way.

From single ascospores derived from the perithecia developed *in vitro*, cultures were made and grown in malt extract agar; the resulting individuals produced *Fusarium* conidia and were identical in every way with the original ascospore cultures, thus confirming the relationship between the two stages in the life history of the fungus described by Pethybridge above.

As will have been seen in the preceding note, there is no record of successful inoculations having been carried out with *Nectria Rubi*, nor is there yet any direct evidence to show that the fungus is definitely parasitic. The investigation of several cases of "Crown Rot" has failed to reveal any trace of *Nectria Rubi* except in isolated instances, *e.g.* from plants from Worcestershire and Long Ashton; on the other hand, *Diaporthe perniciosa* March. is almost always present. Further, "Crown Rot" has so far only been found by the writer to occur in areas that tend to lie wet in the winter. It is possible that prolonged waterlogging such as may occur in an abnormally wet season may set up physiological disturbances in the plant, preventing the normal "plug" formation, and so allowing the entry of fungi such as *Diaporthe perniciosa*. *Nectria Rubi* may act as a follower or may play a joint part in causing the death of the plant. In this connection it is perhaps significant that *Nectria Rubi* was discovered by Pethybridge in 1916 following the wet year of 1915, and it was first found in Scotland and England in 1925 following the wet year of 1924.

Reference may be made here to another fungus of the *Fusarium* type which has been found by the writer on diseased raspberry roots. The conidia of this fungus are borne on white sporodochia which burst through the bark below soil level. Typical conidia differ markedly from those of *Nectria Rubi*. They are smaller, very slightly curved, 3–4-septate and are

attenuated slightly towards one extremity. Average conidia measure $37 \times 5\,\mu$. In size and shape they agree with those of a species of *Fusarium* mentioned by Wormald* as occurring on diseased raspberry roots. This fungus has also been found in association with "Crown Rot"; but it is not considered to have any relation to *Nectria Rubi*, since it differs considerably, not only morphologically, but in cultural characteristics, from the conidial stage of that fungus. Further attention is being devoted to this *Fusarium*.

ADDENDUM.

Since the above notes were written a paper has come to hand from Dr Wollenweber, "Pyrenomyceten-Studien, II" (*Angew. Bot.* VIII (1926), 168), in which some reference to *Nectria Rubi* is made. In *Phytopathology*, III (1913), 211 and 224, Fig. 15, Plate XXII, Wollenweber transferred this fungus to the genus *Hypomyces* because it produces chlamydospores, although not abundantly. It is also listed in that genus in this author's "*Fusaria* autographice delineata" (*Ann. Mycolog.* XV (1917), 8); but in his 1926 paper, mentioned above, it is reinstated in the genus *Nectria*; and *Nectria mammoidea* Phil. et Plow. var. *Rubi* Weese and *Cylindrocarpon janthothele* Wr. are given as synonyms. Although it would appear from the statement on p. 169 of the 1926 paper that Dr Wollenweber regards the fungus as a parasite (*Wurzelschädiger*) of raspberry, in a letter to the writer he admits that this has not yet been proved. Nevertheless, he points out that it belongs to a group of related fungi which are injurious to plants and probably forms no exception.

G. H. P.

THE PARASITISM OF PLOWRIGHTIA RIBESIA ON THE CURRANT†.

By Ismé A. Hoggan, M.Sc. (Cantab.), M.S. (Wisc.)

(With Plates IV–VII and 2 Text-figs.)

INTRODUCTION.

PLOWRIGHTIA RIBESIA (Pers.) Sacc. has long been known as a fungus causing a disease of the currant, and its morphology has been worked out in detail by previous investigators. Little consideration, however, has been given to the pathological aspects of the disease, and the present paper deals with an in-

* Wormald, H. Journal of the South Eastern Agricultural College, No. 22 (1923), 481.

† This work was submitted as a thesis in partial fulfilment of the requirements for the degree of M.Sc. at Cambridge University in 1925.

vestigation carried out primarily from this point of view. The main purpose of the work was to determine the natural mode of infection of the host and the extent to which the fungus might be regarded as a parasite. An account of certain cultural and other studies is included. The work was undertaken on the suggestion of Mr F. T. Brooks, and was carried out under his supervision at the Cambridge Botany School.

Literature.

Tulasne (1) describes various spore forms on the currant which he ascribes to *Dothidea* (*Plowrightia*) *ribesia*. He mentions oval, hyaline conidia which are abstricted in great numbers from stout, closely crowded conidiophores arising from the black pustules of the fungus; small, rod-like spores arising from the walls of irregular cavities in the stroma; perithecia containing asci, and a pycnidial stage externally resembling the perithecial pustules, but producing numerous, small, hyaline conidia which later become dark-coloured and septate.

Brefeld (2) supplements Tulasne's account with a detailed description of the behaviour of the ascospores and conidia in culture. He states that the ascospores send out germ tubes usually from both ends; these abstrict numerous hyaline conidia. Similar conidia may form at the poles and at the septum of the spores before or after germination, while other ascospores germinate purely vegetatively, forming short, profusely branched hyphae which may become dark green in colour. The conidia multiply rapidly by a process of budding, and later proceed to the formation of gemmae. Brefeld doubts the identity of Tulasne's pycnidial forms with *Plowrightia ribesia*, but includes the conidial stage on the stroma on account of the characteristic budding of the spores.

Massee (3) is the first to consider the relation of the fungus to its host. He inoculated two healthy young plants, one gooseberry, one red currant, from material of the fungus obtained upon gooseberry, "by introducing spores into incisions made in the bark." After seven weeks the infected parts appeared dry and shrivelled, and within three months pustules of the fungus developed to a distance of one inch above and below the point of inoculation. Since no infection was obtained by placing spores on uninjured bark, he concludes that the fungus is a wound parasite. Later (4), he writes: "...in all probability aphids or scale enable the parasite to gain an entrance into the living tissues of the host." He states that wilting and yellowing of the foliage is the first indication of the disease, and that the branch is usually killed the second year after infection owing to the water-supply being cut off by the development of mycelium in the vessels. He

mentions gooseberry and red and black currant as hosts, and states that the fructifications do not appear until the branch is quite or nearly dead.

Field Observations.

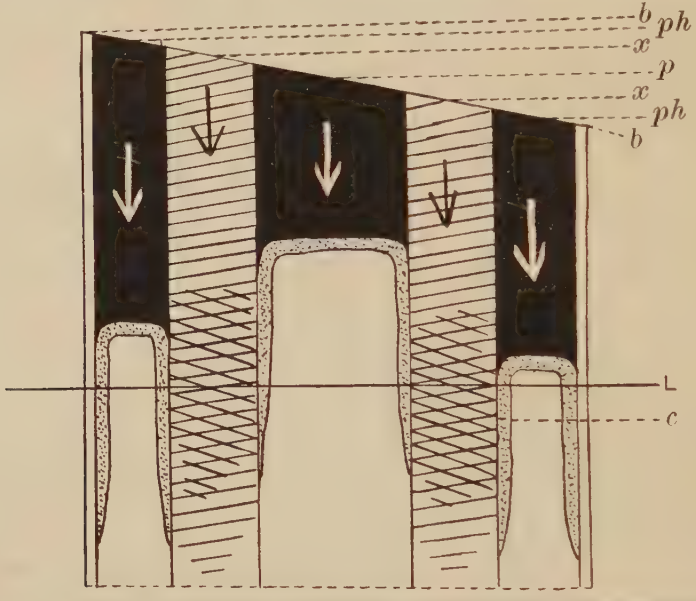
The disease was found to be of common occurrence on red currant, and less frequent on black currant. No infected gooseberry bushes were observed by the writer. The characteristic symptoms of the disease are isolated, dead branches bearing the black lenticular or oval stromata of the fungus (Plate IV, fig. 1). These stromata break through the bark in late summer and develop perithecia during the winter months. The spores are delimited in the asci about January and reach maturity about the following April.

Usually from one to several infected branches are found upon otherwise healthy bushes, while sometimes the main axis is attacked and the entire bush killed. Such bushes are generally relatively old or grown in neglected orchards. Some hundreds of bushes were examined in various orchards—chiefly red currant—and a very high percentage of these proved to be diseased. With three exceptions, which will be considered later, each diseased branch had previously been pruned back or was directly connected with a second infected branch which had been pruned. This suggested that the fungus might effect an entry through the cut surfaces left in pruning, but gave no indication whether infection could occur through unbroken surfaces. The diseased twigs were infected to distances of from one quarter of an inch upwards from the cut surface, the entire spur frequently being invaded. The infected portions were shrivelled and bore fructifications of the fungus; a sharp line of demarcation could be distinguished externally between the diseased and healthy regions of the stem. It was evident here that the fungus had entered at the cut surface and was working back towards the base of the spur.

Certain other fungi were commonly found associated with the *Plowrightia*, such as *Cladosporium* and *Alternaria*; by far the most frequent was the coral-spot fungus, *Nectria cinnabarina*, which was encountered so regularly at one period that it became exceptional to find material of *Plowrightia* free from this fungus. The red pustules were scattered among the black stromata of the *Plowrightia*, and frequently arose at either end of the stromata, contiguous with them, or pushing up immediately beneath them and even enclosed within them. It seemed possible that *Nectria* might prepare the way for subsequent infection by *Plowrightia* and one series of inoculations was carried out to test this possibility.

Pathological Histology.

The mycelium of the fungus presents a very characteristic appearance in the stems and is easily recognised (Plate V, fig. 2). The hyphae are extraordinarily stout when mature, as much as 20 μ or more in width, and grow in the cells in a very twisted and gnarled manner; they have numerous septa and are deep olive green or brown in colour. The young hyphae are hyaline, much narrower, and take up stains readily. The mycelium invades all tissues of the stem within the bark, being particularly

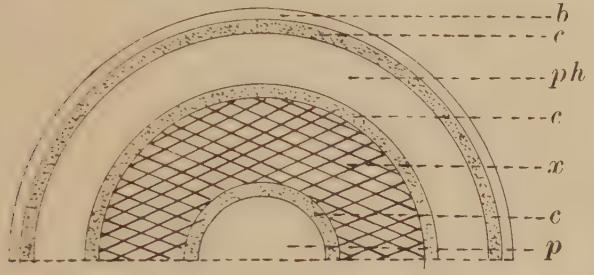


Text-fig. 1. Diagram illustrating formation of cork layers in diseased stem of red currant. Radial longitudinal section. *b*, bark; *c*, cork; *p*, pith; *ph*, phloem; *x*, xylem. Black areas represent diseased tissue, white areas healthy tissue and shaded areas regions of wood with resinous contents. Arrows indicate direction of progress of mycelium.

abundant in the phloem and pith, causing a dry rot of these tissues. Here the hyphae grow in a dense, tangled mass; in the wood they are less abundant and pass from one cell to another through the pits in the walls. They appear to travel in a vertical direction through the vessels and tracheids, and horizontally through the medullary rays (Plate V, figs. 2 and 3). The diseased pruned twigs which were infected part of the way down from the cut surface invariably showed the formation of certain layers of cork at the junction of the diseased and healthy tissues, corresponding in position to the line of demarca-

tion between the two regions previously mentioned. The position of these cork layers will be understood best from the above diagrams (Text-figs. 1 and 2).

One layer stretches completely across the pith in a horizontal direction to the wood, then curves sharply downwards and runs vertically downwards for a considerable distance immediately inside and adjacent to the protoxylem, or in some cases between the protoxylem and the metaxylem, thus forming a complete cylinder of cork enclosing the pith and closed at the top. This bars the passage of mycelium from the wood outside or from the diseased pith above, into the healthy pith inside the cork cylinder (Text-fig. 1). Similar formations occur in the phloem, consisting of a horizontal sheet of cork extending from the bark to the outer edge of the wood, and running vertically downwards between the bark and the outer edge of the phloem, and



Text-fig. 2. Transverse section of same at level *L*. Lettering as in 1.

between the inner edge of the phloem and the wood (Text-figs. 1 and 2). This blocks the way of the mycelium from above or from the side into the healthy phloem area within the cork layers. The wood at this level is much discoloured by masses of resinous substances secreted in the vessels and medullary rays. Since no hyphae could be detected in these discoloured regions it seemed as though the resinous substances also serve as a barrier to the advancing mycelium, so that further progress down the stem is prevented in all parts. In some twigs, however, two or three such series of cork layers may be found at different levels, the lowest separating the healthy and diseased tissues as before, the others situated within the diseased region of the stem, suggesting that in some way the mycelium had been able to evade the barrier of cork and resin and penetrate further into the host. This will be referred to again later.

Inoculation Experiments

The field observations above recorded led one to suspect that the pruning wounds served as a point of entry for the fungus,

but gave no indication whether normal healthy branches were also susceptible to infection. Experiments were therefore carried out to determine the susceptibility to infection of the following:

1. Healthy branches.
2. Artificially pruned branches.
3. Artificially killed branches.

Both mycelium and ascospores were used as sources of inoculum. Pure cultures of mycelium were obtained by the following method. Stromata were sterilised by immersion in a one per cent. solution of mercuric chloride for fifteen seconds, and washed in sterile distilled water. Sections were cut with a sterile razor and plated out on red currant wood-extract agar in Petri dishes. An abundant mycelium developed in a few days and was transferred to sterile portions of red currant stems where it grew luxuriantly. The ascospores were obtained by suspending sterile coverslips over mature moistened stromata in sterile Petri dishes, when the spores were shot upwards and collected on the coverslips. From these a spore suspension in water was made. Red and black currant bushes three or four years old were used for inoculation purposes, and were grown in large pots in the open.

(1) *Inoculation of healthy branches.* The inoculum was inserted into deep wounds made with a sterile knife into healthy, growing branches, and the wounds were immediately covered with tin foil and bound with wool. When mycelium was employed, a drop of sterile water was added with the inoculum. When ascospores were used, germination tests were carried out at the same time to prove that they were viable. The results are summarised in Table I.

Table I. *Inoculation of healthy branches of currant.*

Inoculum	Host	No. of inoculations	No. of infections
Mycelium	Red currant	34	0
Mycelium	Black currant	20	0
Ascospores	Red currant	16	(2)[1]
Ascospores	Black currant	16	0

[1] These two infections were obtained on branches which were not in a healthy condition at the time of inoculation.

With two exceptions, no infection resulted from these inoculations, the branches remaining healthy after six to twelve months. In the two exceptional cases where infection was obtained, branches had purposely been selected which appeared in a moribund condition with yellowing leaves, though showing no

further symptoms of disease and arising from apparently healthy branches. They cannot, however, be included in the category of normal healthy branches.

Microscopic examination of other inoculated twigs revealed a small patch of discoloured tissue surrounding the wound, consisting of dead phloem and pith cells and wood elements with resinous contents, these frequently being bounded by an irregular cork layer. A certain amount of mycelium was present in the discoloured region, and this was still living, as subsequent plating-out tests demonstrated, but was evidently unable to spread.

(2) *Inoculation of artificially pruned branches.* Healthy branches were cut back with a pruning knife and inoculum placed immediately on the cut surface and covered with tin foil, or the cut surfaces were covered at once and inoculated later after intervals varying from one to nine weeks after pruning. The results are given in Table II.

Table II. *Inoculation of artificially pruned branches of currant.*

Inoculum	Host	Interval between pruning and inoculation	No. of inoculations	No. of infections
Mycelium	Red currant	0	10	0
,,	Black currant	0	10	0
Ascospores	Red currant	0	16	14
,,	Black currant	0	8	6
,,	Red currant	1 week	8	5
,,	,,	2 weeks	8	7
,,	,,	3 ,,	8	8
,,	,,	4 ,,	8	6
,,	,,	6 ,,	8	6
,,	,,	9 ,,	8	6
,,	Black currant	9 ,,	8	5

Inoculation with mycelium gave negative results, but with an ascospore suspension, of a total of eighty inoculations, sixty-three gave positive results, the twigs becoming infected to distances of half an inch and upwards from the cut surfaces and developing fructifications three to five months after inoculation. The diseased twigs closely resembled the naturally infected pruned twigs previously described, showing a shrivelled diseased portion and a sharp line of demarcation between the healthy and diseased tissues, where a similar development of cork layers had occurred. No further spread of mycelium took place beyond this point during the winter months, the inoculations having been performed in May and early June. The following summer, in a single twig, the mycelium worked past the cork zone and invaded the entire branch, fructifications developing on the newly infected area. No further spread of mycelium occurred, however, on any of the other inoculated spurs.

In order to follow more closely the progress of infection by the ascospores, a number of healthy branches were removed from red currant bushes, the tops cut back, and the cut surfaces inoculated immediately with a spore suspension. The twigs were kept in the laboratory under moist conditions and hand sections were examined microscopically at twenty-four hour intervals for a week. Twenty-four hours after inoculation, a number of ascospores had begun to germinate. These lay on the surface of the cut, or in the wood vessels at a short distance below the surface. Others had abstricted numerous bud spores, a few of which later produced germ tubes which penetrated the tissues of the stem. After three days an abundant mycelium had developed from the ascospores, the hyphae invading the vessels, the pith and the phloem to a depth of about two millimetres, growing at first more rapidly in the wood elements but after a week or more becoming more abundant and progressing slightly more rapidly in the phloem and pith. The mycelium then spread rapidly throughout the stem, and if these were kept sufficiently moist, fructifications developed on the surface within two months. In the early stages of infection the mycelium was strictly intercellular in the pith and phloem, only entering the cells after they were killed; in the wood the mycelium was intracellular.

(3) *Inoculation of artificially killed branches.* Healthy branches were killed by subjecting the base to a steam jet for several minutes, and after a few weeks, when the leaves had shrivelled, wound inoculations were made one or more inches above the steamed region. Inoculations were also made with mycelium of *Nectria cinnabarina* alone and in combination with mycelium of *Plowrightia* to determine whether the former bore any relation to infection by *Plowrightia*. The results are summarised in Table III.

Table III. *Wound inoculation of artificially killed branches of red currant.*

Inoculum	No. of inoculations	No. of infections
Ascospores of *Plowrightia*	12	10
Mycelium of *Plowrightia*	24*	18
Mycelium of *Plowrightia* and of *Nectria*	4*	3 (*Nectria*) 0 (*Plowrightia*)
Mycelium of *Nectria*	4*	3
Mycelium of *Plowrightia* followed 3 months later by mycelium of *Nectria*	4*	3 (*Nectria*) 0 (*Plowrightia*)

* One inoculation made at a distance of one inch from the steamed area, this giving negative results.

Infection was obtained from both mycelium and ascospores of *Plowrightia*, fructifications developing within three months

above and below the wound. When, however, *Plowrightia* was inoculated together with, or subsequent to infection with *Nectria*, it failed to develop. Where an inoculation was made at a distance of one inch from the steamed area, infection in no case resulted, no matter what the inoculum.

Discussion.

The inoculation experiments recorded above indicate that *Plowrightia ribesia* is unable to infect normal healthy branches of the currant, even when these are wounded, but that infection by ascospores readily takes place through spurs left in pruning. That this is a common mode of infection in nature is indicated by the field observations previously described. The experiments further demonstrate that the fungus readily invades moribund tissue, and it appears probable that it must in every case establish itself first upon such tissue before being capable of attacking the living portions of the host. When a twig is pruned, the upward flow of sap is checked, and the remaining spur will gradually die back from the tip. Hence dead or dying tissue is formed which is freely exposed to the ascospores of the fungus and in which it can gain a footing. It has been shown that, once established, the mycelium can work backwards into the stems, gradually invading the living tissues until the way is barred by the cork and resinous layers which later develop in the stem. In this way *Plowrightia* behaves as a weak "wound parasite," in a manner very similar to *Nectria cinnabarina* upon the currant, as described by Line (5). It has further been shown that the mycelium is able in some way to evade the cork barrier and resume its progress down the stem. It is unlikely that the hyphae could pass through the cork layer itself, and the only alternative way is through the xylem elements in which resinous materials have developed. Hiley (6) discusses a similar situation with regard to *Dasyscypha calycina* on the larch, and concludes that the mycelium either slips through between the cork and the wood, or through the wood itself, though he did not observe any mycelium in either of these positions. In the isolated instance recorded above of inoculation of artificially pruned branches where the mycelium penetrated beyond the cork barrier, microscopic examination subsequently revealed the presence of a few hyphae of the fungus running down through the vessels in the discoloured region of the wood. It is therefore concluded that the mycelium can and does grow down through this area of the wood and so works downwards towards the base of the branch. The cork layers develop in late summer when the growth of the fungus is presumably slowing up or has

already ceased. The next spring would bring a renewal of activity on the part of the fungus which might enable it to penetrate the barrier.

The ascospores are liberated from the perithecia under natural conditions from the end of April to the middle or end of June. It appears to be a common practice in England to prune the currant bushes at the end of the winter season, generally some time in March. It has been shown that the ascospores can infect the spurs at least nine weeks after the twigs have been pruned, so that spurs left after a pruning in March are susceptible to infection by spores liberated in April and May, and in all probability to those liberated later than this.

The inoculation experiments carried out with *Plowrightia* and *Nectria* indicate that the latter does not prepare the way for secondary infection by *Plowrightia*.

Massee concludes that the death of the twigs is due to a plugging of the vessels, and the present writer has observed vessels almost completely filled with the wide hyphae of the fungus. Frequently, however, the wood appears to be relatively free from mycelium, though this is always abundant in the pith and phloem, and it appears possible that some toxic action of the fungus is responsible, at least in part, for the death of the host tissues.

With regard to the three isolated cases recorded of field observations of natural infection of branches which were not pruned nor connected with diseased branches, it is probable that these were in a weakened or dying condition through some acuse, and became infected through a wound. Two of the three bore large scars where lateral branches had fallen off, and the third had a twisted top characteristic of aphid injury. The experiments recorded above demonstrated that moribund branches can be infected by ascospores through wounds and it is probable that this had occurred in these three diseased twigs. It is possible, as Massee suggests, that aphid or scale injury may be associated with infection in certain cases; however, direct infection through pruned spurs appears to be the usual method in nature. The presence of aphids or scale was rarely noted in the orchards kept under observation during two summers, while the disease became widely distributed.

Cultural Work.

When sections of sterilised stromata were plated out by the method already described for the preparation of pure cultures of the fungus, a profuse mycelial growth was obtained upon red currant wood-extract agar, and from which numerous oval

conidia were abstricted. These cultures agreed closely with the descriptions given by Brefeld (*loc. cit.*), and his account of gemma formation by the spores was likewise confirmed.

The nature of the medium employed was found to exert considerable influence upon the method of germination of the ascospores. In distilled water, numerous conidia were abstricted from either end of the spore and at the septum, but germ tubes never developed. On red currant wood-extract agar, and in beer-wort, hyphae were formed at one or both ends of the spore. If from one end only, it was invariably the larger of the two cells which germinated; if from both ends, the larger cell began to germinate before the smaller. Frequently hyphae arose laterally also. Conidia were usually abstricted after germination had begun, in numbers varying considerably with the strain employed. Ascospores germinating in agar plates in Petri dishes gave rise to circular, white, mycelial colonies which produced enormous quantities of conidia for a time, after which the hyphae continued to grow purely vegetatively and bore no more conidia (Plate VI, fig. 7). Conidia plated out in a similar medium gave rise to somewhat similar colonies if germinating within the agar; if, however, the conidia germinated on the surface of the medium, a circular, white colony developed at that point, consisting entirely of mucilaginous bud spores, and no mycelium, somewhat resembling a bacterial colony and increasing in size up to several millimetres in diameter (Plate VI, fig. 8).

Attempts to produce mature fructifications in culture, with perithecia and ascospores, were unsuccessful. At ordinary laboratory temperatures, the cultures on red currant wood-blocks consisted of a dense, fluffy, mycelial growth, olive-green in colour, in which there developed later certain black, elongated, club-shaped structures (Plate VII, figs. 9 and 10, *c*), sometimes forked, and up to three millimetres in length. These were composed of dark coloured, densely woven hyphae, but developed no trace of perithecia. Cultures on red currant wood with a one per cent. solution of glycerine, on potato and carrot chunks, and on potato chunks with one per cent. glycerine gave no better results, only mycelium developing on the last three media. It was observed that at lower temperatures these organs assumed a more compact form, the microscopic structure closely resembling that of a natural stroma, consisting of a fairly compact, dark-walled parenchyma. Young cultures were therefore placed on the roof of the laboratory for six weeks or more during January and February and exposed to temperatures falling as low as 10° F. At the end of this time, black, oval, or hemispherical pustules had developed with a definitely papillose surface and an internal structure similar to that of a natural stroma, showing

a slight differentiation of thin-walled chambers comparable to the early stages of development of the perithecia (Plate VII, fig. 11, *p*). No further development of these bodies was, however, obtained, either from single spore cultures or from various combinations of these. Occasionally the bodies gave rise to a slimy, white mass of bud spores (Plate VII, fig. 9, *b*), which arose from the tips of thick hyphae at the surface of the organs, in a manner similar to that described by Tulasne (*loc. cit.*), where stout conidiophores arising from the black pustules of the fungus abstricted conidia in great numbers.

These club shaped organs appear to be similar to certain branched, stalk-shaped bodies obtained in cultures of *Brachysporium Trifolii* by Lee Bonar (7). Some of these bore conidiophores and conidia at the tip, while others formed an internal differentiated region comparable with the development of perithecia in the Pyrenomycetes. As with the *Plowrightia*, however, no asci nor ascospores were produced.

Spore Liberation and the Mechanism of the Ascus.

Since infection of the currant is brought about by the ascospores of the fungus, it was essential to know how and when these are liberated. Portions of bark bearing mature perithecia were placed in Petri dishes containing damp filter-paper and a glass ring of the type used for hanging-drop cultures, about half an inch in diameter, was placed round each fragment of bark and a coverslip laid across the top. After several hours the coverslips were removed and examined under the microscope, when quantities of ascospores were found to have collected on the under surface of the glass. Mature perithecia placed similarly in Petri dishes, but kept dry, retained their spores indefinitely, the coverslips remaining without spores for weeks. Subsequent addition of moisture invariably produced a copious ejection of spores on to the glass; it was therefore evident that moisture was essential to spore liberation, as, for example, with the chestnut blight fungus, *Endothia parasitica* (8), and the apple-scab fungus, *Venturia inaequalis* (9).

In order to study the actual process of spore discharge from the ascus, moistened stromata were crushed on a glass slide as soon as spore discharge had begun, and numerous ripe asci were obtained in this way lying freely and intact in a thin film of water under the coverslip. It subsequently appeared that the ascus wall consists of two layers, the outer exceedingly thin and more or less inextensible, the inner relatively thick, capable of great extension and of swelling up enormously on coming into contact with water. The two layers are, however,

indistinguishable in the mature ascus until the process of spore discharge begins.

After some minutes of immersion in water, the outer of the two walls ruptures suddenly at the tip, and the inner wall with its contents immediately pushes through the aperture, elongating rapidly in sudden jerks, with a forward sliding motion, until in a few minutes it has extended to two or three times the original length of the ascus (Plate V, fig. 4, *a*, *b*, *c*). No appreciable increase in width, however, occurs. The ascospores are carried up in the process of elongation and come to lie in a single irregular row throughout the length of the ascus, the uppermost usually situated right at the apex, and the lowest wedged in the short basal stalk whence it is frequently not dislodged. When the extension is complete, a pause of several minutes follows; the apex of the inner wall then suddenly ruptures and the tip of the first spore is forced through the small hole formed at the apex (Plate V, fig. 4, *d*). Prior to the rupture, a slightly thinner area in the wall can sometimes be discerned at this point, and this occasionally swells up into a tiny, knob-like protrusion before bursting. The form of the ascospore evidently plays a part in the discharge which follows. The spore is two-celled, the upper cell being longer and broader than the lower; each is pear-shaped, with the pointed ends forming the poles of the spore (Plate V, fig. 4, *d*). Hence the greatest width comes about halfway between the poles and just above the septum. The spore is gradually forced out of the opening until the maximum diameter is reached, when it is shot out from the ascus with considerable violence and is replaced immediately by the second spore. The performance is then repeated for each spore, the eighth frequently remaining fast in the basal stalk. The spores follow one another at intervals of one or more seconds, and sometimes a definite contraction and re-elongation of the ascus may be observed after each successive discharge. As the last spore is shot out the ascus collapses, shrinking rapidly to about two-thirds of the maximum length, while at the same time the inner wall swells up as if gelatinous, until only a very narrow lumen remains (Plate V, fig. 4, *e*). In order to determine what takes place within the perithecium containing numerous, closely crowded asci, longitudinal sections of mature stromata were cut by hand, mounted in water and examined under the microscope. The ripe asci were packed closely together, arising from a pad of small, thin-walled, hyaline cells at the base of the perithecium and extending to the roof of the chamber. As soon as spore discharge began, the asci upon elongation pushed up through the narrow ostiole and protruded above the surface of the stroma to a distance of about one-third of their total

length (Plate V, fig. 5). After the spores were expelled, the empty ascus shrank back completely within the perithecium, and was replaced by another about to discharge its spores.

Entire stromata which had been moistened and from which spores were being copiously liberated, were viewed in profile under the low power of the microscope. The tips of the elongating asci could clearly be seen emerging from the papillose mouths of the perithecia, the walls of the ascus being sufficiently transparent to reveal the spores lying within. As soon as the tip ruptured, the spores were shot out in rapid succession, as fast as one could count, and without any appreciable pause. Usually all eight spores were ejected, the ascus giving a backward jerk as each spore left the opening, and shrinking back within the perithecium as the last spore was expelled. Generally only one ascus projected from the ostiole at any given moment, though occasionally two or even three were observed together occupying the mouth of the perithecium. Presumably a similar process occurs under natural conditions.

A further method was devised in which stromata were moistened and placed within a glass ring with a coverslip laid across the top. Spores shot upwards from the perithecia adhered to the coverslip and could be observed under the low power of the microscope arriving on the glass surface as glistening bodies on a dark ground and giving a very pretty effect. The shortest interval observed between the moistening of the stromata and the onset of spore discharge was twenty minutes. The rate of discharge was slow at first, but rapidly increased until after an hour or so had elapsed, and spores were being liberated in great quantities. By frequent changing of the coverslip, the position of each spore could be noted. The spores arrived in small groups, the members of a group following one another in rapid succession, and presumably representing the contents of a single ascus. A considerable divergence was observed in the direction of the spores expelled from any one ascus, the maximum distance observed between two such spores on a coverslip placed five millimetres above the mouths of the perithecia was estimated at about 0·5 mm., or twenty times the length of the spore. Groups of eight were rarely observed. This may have been due to the fact that all eight spores were not discharged from the ascus, or, more probably, that they were not all discharged with sufficient violence to reach the coverslip. Possibly, also, the divergence in direction between the spores was so great that some were erroneously not included in the group in question.

The maximum vertical height to which the spores were shot was determined by superimposing two or more glass rings of

varying depth and placing a coverslip across the top. This distance was estimated at about one centimetre, which agrees with similar measurements made by Aderhold (9), with the ascospores of *Venturia inaequalis*. The maximum horizontal distance to which the spores were projected was found to be about three centimetres.

The violent ejection of spores from the ascus is quite a common feature in Ascomycetes, though in many cases the eight spores are expelled simultaneously in a single mass. The successive discharge, such as that described above, is known to occur in some forms, chiefly among the Pyrenomycetes. Pringsheim (10) reports an almost identical process of spore discharge in *Sphaeria Scirpi*, and Hodgetts (11) in *Leptosphaeria acuta*, where, however, actual ejection of the spores did not occur when the asci were submerged in water. Aderhold (9) speaks of asci which elongate prior to spore discharge in *Venturia inaequalis* and *V. pirina*. Lindau in Engler and Prantl (12), gives the presence of a double wall as a character of all members of the Pleosporaceae, which group includes *Leptosphaeria*, *Sphaeria* and *Venturia*. Tubeuf (13) describes a similar spore discharge mechanism in *Cucurbitaria Laburni*. Further mention of elongating asci is made by Zopf in *Sordaria* and Klebahn in *Mycosphaerella punctiformis* (14), and it is possible that this type of spore discharge may prove to be a common feature of the Sphaeriales, a group to which all these forms belong. In any event, it is of interest to find an identical method of spore discharge in *Plowrightia ribesia*, which is classed among the Dothideales, and suggests a possible close relationship between these two groups.

That the spores are liberated in nature only after rain was demonstrated by clipping glass coverslips on to diseased twigs over the stromata. These received a copious deposit of spores after the branches had been wetted by a rain shower, but received no deposit in dry weather.

Since the asci project beyond the mouth of the perithecium prior to spore discharge, the spores are of necessity ejected into the air, and are presumably disseminated by wind. As they are liberated only in moist weather, suitable moisture conditions will be present for their immediate germination provided that they alight upon a suitable host before sufficient time has elapsed for its surface to dry up again. This method of spore liberation appears therefore to be adequate in all respects and highly favourable to the spread of the disease.

The actual mechanism of dehiscence of the ascus and of spore ejection is in all probability due to the development of a very high turgor pressure within the ascus. It is significant that the

process occurs only in the presence of abundant moisture. Water presumably passes through the walls into the cell and raises the internal pressure until the rigid outer wall can no longer withstand the strain and ruptures at the point of least resistance. The external pressure on the inner wall is now released, and as this consists of an extensible material, rapid elongation follows. If water continues to be absorbed through the inner wall of the ascus, the breaking point of this will eventually be reached, and rupture will occur at the weakest point, *i.e.* the apex. Treatment of the mature ascus with Schultze's solution causes a definite shrinkage, the wall swelling up somewhat, the increase in width being uniform except at the apex. Here a small area at the extreme tip remains relatively thin (Plate V, fig. 6), while the adjacent portions become thicker than elsewhere. A similar irregularity in width was observed in the walls of very young asci, suggesting that there is a weaker region at the tip which would account for the rupture always occurring at that point. Tubeuf (*loc. cit.*) and Hodgetts (*loc. cit.*) figure similar variations in thickness in the ascus wall in *Cucurbitaria Laburni* and in *Leptosphaeria acuta*.

The violent expulsion of the spores may be due partly to the high pressure set up within the ascus and partly to a lateral pressure exerted through the elastic contraction of the rim of the aperture. Attempts made to differentiate the two layers in the wall of undischarged asci by stains were not successful, though these showed clearly in the collapsed asci after discharge, particularly when mounted in Congo red.

Conclusions.

Infection of the currant by the fungus *Plowrightia ribesia* is brought about by ascospores liberated into the air in early summer by means of a highly specialised mechanism of spore discharge, and disseminated chiefly by wind. Infection takes place mainly through spurs left in pruning, the fungus acting as a weak wound parasite. Normal, healthy branches are not susceptible to infection, though dying branches may be infected by artificial inoculation.

The disease is of common occurrence in English orchards, and, though not usually of great severity, causes a reduction in yield due to the loss of certain of the branches, and may even occasion the death of the entire bush. The control measures to be recommended are simple, namely, to prune back to the surface of the parent branch instead of leaving "snags," and to cut out and destroy all infected branches, since these serve as a place of over-wintering for the fungus and as a source of inoculum the following season. Cultural practices which tend

to keep the bushes in a healthy and vigorous condition are also of value.

I wish in conclusion to record my thanks to Mr F. T. Brooks for his advice and constant supervision of the work, and to Mr W. Tams, who took the photographs here reproduced.

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EXPLANATION OF PLATES IV–VII.

All drawings were made with the aid of a camera lucida.

Plate IV.

Fig. 1. Dead stems of currant infected with *Plowrightia ribesia* and bearing mature fructifications of the fungus. (*a*) black currant, (*b*) and (*c*) red currant. Slightly reduced.

Plate V.

Fig. 2. Radial longitudinal section of diseased stem of red currant showing mycelium (*m*) of *Plowrightia ribesia* in the xylem and pith. *x*, xylem; *p*, dead pith cells. × 300 approx.

Fig. 3. Tangential longitudinal section of diseased stem showing mycelium (*m*) in medullary ray. × 300 approx.

Fig. 4. Stages in spore discharge from mature ascus in water:
(*a*) Mature ascus before elongation.
(*b*), (*c*) Stages in elongation.
(*d*) Commencement of spore discharge.
(*e*) Collapsed ascus after discharge, showing swollen inner wall of ascus. × 100 approx.

Fig. 5. Longitudinal section through mature perithecium showing elongation of asci in water. × 70 approx.

Fig. 6. Mature ascus after treatment with Schultze's solution, showing irregular thickening of wall at apex. × 225 approx.

PLATE VI.

Fig. 7. Development of colonies from ascospores on red currant wood agar. Slightly reduced.
Fig. 8. Development of colonies from bud spores on red currant wood agar. (*a*) surface colony consisting entirely of bud spores; (*b*) submerged colony of mycelium bearing conidia. Slightly reduced.

PLATE VII.

Fig. 9. Mycelial culture on sterilised red currant wood, kept at room temperatures, showing development of club-shaped organs at (*c*), and masses of bud spores arising from similar organs at (*b*). Slightly reduced.
Fig. 10. Younger culture showing mycelial growth and developing club-shaped organs at (*c*). Slightly reduced.
Fig. 11. Mycelial culture after six weeks' exposure to low temperatures on roof of laboratory. Perithecial body at *p*. Slightly reduced.

STUDIES IN ENTOMOGENOUS FUNGI.

XII. PEZIOTRICHUM LACHNELLA; OPHIONECTRIA COCCORUM; VOLUTELLA EPICOCCUM.

By T. Petch, B.A., B.Sc.

(With Plate VIII.)

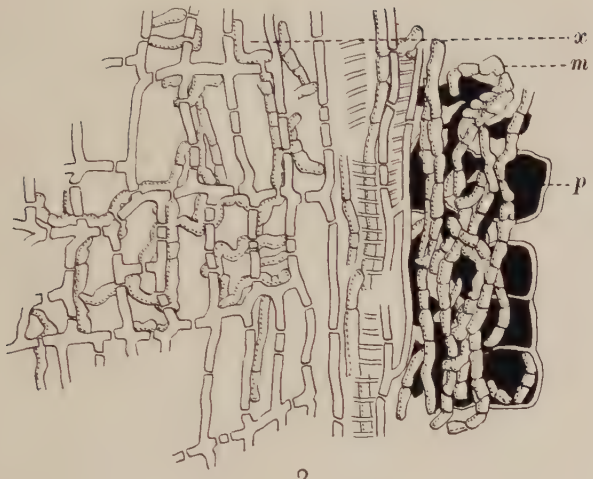
THE three fungi dealt with in this paper are so remarkably similar in general appearance that a genetic relationship between them is immediately suspected. As regards two of them, this has been established by a series of specimens, but no link has yet been found between these and the third. Endeavours to obtain pure cultures have proved abortive.

Peziotrichum Lachnella Sacc.

Parkin in 1906 described a Hyphomycete which was found by Mr E. E. Green on *Hemichionaspis aspidistrae* on a palm at Peradeniya, October, 1899, and on *Aonidia* sp. on leaves of *Memecylon* at Elephant Pass, Ceylon. He referred it to the genus *Peziotrichum* Sacc. I have specimens of both those collections, and others on *Hemichionaspis aspidistrae* on *Fagraea zeylanica* from Peradeniya, and on a Diaspid on *Bambusa* sp. from Malabar (India).

In the specimens on *Hemichionaspis* (Plate VIII, fig. 1) the fungus forms a thin, brown mat over the scale, and spreads out in radiating hyphae closely adherent to the leaf, thus forming a thin, byssoid, rufous-brown stroma, up to 2 mm. in diameter. The marginal radial hyphae of the stroma are rather widely separated, straight, septate, dark yellow-brown, 4–7 μ diameter: they branch at an acute angle, the branches being also

I
Plowrightia ribesia.



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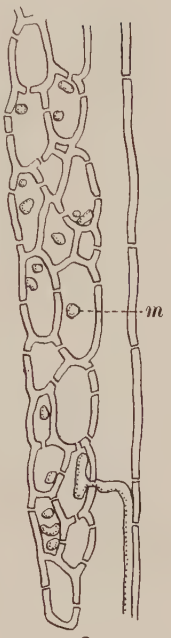

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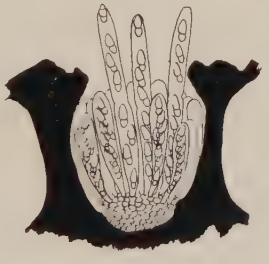

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Plowrightia ribesia.

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8

Plowrightia ribesia.

Plowrightia ribesia.

directed radially. In addition, these main hyphae give off curved or flexuose lateral branches, which may remain short and simple, or may branch repeatedly, and by the interweaving and fusion of these branches the radial hyphae are united into a continuous stroma. Some of the flexuose hyphae diminish to a diameter of 2 μ.

The branches frequently terminate in spore-like bodies (Plate VIII, fig. 2), either globose, 14–18 μ diameter, or oval, 18–20 × 14–16 μ, yellow-brown, usually thin-walled. In some cases, these bodies are thick-walled, or the wall may be thick at the base and become thin over the distal hemisphere. These bodies lie in the stroma among the interwoven hyphae. They are somewhat scattered along the individual hyphae, but appear more crowded when the stroma is viewed as a whole, owing to the intermingling of the branches from adjacent hyphae.

Round the edge of the scale there arise numerous, erect, rigid, dark rufous-brown setae (Plate VIII, fig. 5). These are up to 2 mm. high, 4–10 μ diameter, yellow-brown or blackish brown, septate, thick-walled. In general, the apex is slightly inflated, elongated oval, thin-walled and hyaline, as if immature, but some setae are attenuated above and terminate in an acuminate tip. These setae arise singly from the repent hyphae, and fuse laterally into terete fascicles, tapering upwards, 20 μ diameter, or into triangular fascicles, 200 μ broad at the base. When the scale insect is clearly visible, *i.e.* when there is only a slight covering of hyphae over the scale, the fascicles of setae are situated in an oval or circle round the margin of the scale; but if the insect is covered by a denser stroma, they may arise anywhere on the stroma.

The fungus consequently consists, in general, of a byssoid stroma overlying the scale, a ring of setae round the periphery of the scale, and an extension of the byssoid stroma over the surrounding surface of the leaf. The spore-like bodies lie principally in the stroma, external to the ring of setae.

The specimen from Elephant Pass agrees in all essential details with those from Peradeniya. The stroma, however, is denser, and does not extend so far over the leaf. For that reason, the globose bodies are not so readily seen. The differences are no doubt due to the locality, Elephant Pass being in the dry zone of Ceylon.

Saccardo instituted *Peziotrichum* as a subgenus of *Botryotrichum* in 1893 (*Hedwigia*, XXXII, p. 58), stating at the same time that it should probably be regarded as a new genus. It was apparently raised to generic rank by Lindau in Engler-Prantl, *Pflanzenfamilien*. The fungus on which the genus was founded occurred on living branches and spines of *Bursaria*

spinosa, in Victoria, Australia. Saccardo stated that the fungus recalled *Lachnella barbata*, and hence he named it *Botryotrichum* (*Peziotrichum*) *Lachnella*. His description and figures leave scarcely any room for doubt that the Ceylon fungus is the same species. He gave the height of the sterile hyphae, or setae, as 0·7 mm. only (Parkin gave 0·8–1 mm.), their diameter as 3–4 μ, and the "conidia" as 12 μ, subhyaline. The Ceylon specimens have stouter setae and larger "conidia," the latter being hyaline at first.

Saccardo's figure of the fungus, natural size, shows minute groups of setae on the stem, etc., of a living twig. His enlarged figure of the whole fungus shows erect setae arising round a bare oval space. This second figure was copied into Engler-Prantl, and modified in such a way that the copy gives quite an erroneous idea of the fungus. Regardless of the first figure, which shows the fungus on a living branch, the copyist added to the second figure a piece of wood as a substratum, and by so doing completely altered the perspective of the drawing. The oval ground plan of Saccardo's figure becomes an elevation in the copy, so that the fungus is represented as a pulvinate mass, surrounded by setae; and this appearance is heightened by the introduction of a slight bend in the proximal setae at the level of the upper edge of the apparent stroma. A copy of Saccardo's figure is given here (Plate VIII, fig. 3), together with his figure showing the setae and the repent basal hyphae with globose conidia (Plate VIII, fig. 4). The fungus does not consist of a central group of conidiophores, surrounded by setae, like a *Volutella*, as suggested by the figure in Engler-Prantl, but of a ring of setae, round a scale insect, with repent hyphae, bearing globose conidia-like bodies, extending outwards over the host plant.

The genus *Botryotrichum*, to which Saccardo referred his fungus, contains a single species, *Botryotrichum piluliferum* Marchal. This has been studied by Blochwitz, who found that the figure of that fungus in Engler-Prantl was incorrect, and the current idea of it was totally different from reality. It has hyaline conidia and conidiophores, and does not belong to the Dematiae, where it has hitherto been placed (Blochwitz, A., *Ann. Myc.* XII (1914), 315–334). But Blochwitz added that no one could doubt, from Saccardo's figures and description, that *Peziotrichum* was exactly the same thing, the mycelium having been described as dark from its general appearance, not after microscopical examination. The latter assumption was scarcely justified, seeing that Saccardo figured the mycelium; and the reference of *Peziotrichum Lachnella* to *Botryotrichum piluliferum* is not correct.

To add to the difficulty of interpreting Saccardo's fungus, Lindau described it in his key as having cylindrical conidia. Consequently, Parkin stated that the Ceylon fungus differed from *Peziotrichum* in having spherical, rather than cylindrical or rod-shaped conidia.

The spherical spore-like bodies do not appear to be conidia. They do not become detached from the hyphae, and they have not been got to germinate. They lie among the hyphae, usually in contact with the leaf, but, nevertheless, they do not appear to be hyphopodia.

Similar globose bodies occur in the fungus figured on Plate VIII, fig. 15. This, which was found on a scale insect on *Calophyllum Burmanni* in the Haliella Forest, Ceylon, forms a thin, dark brown stroma over the insect, with fine strands radiating from it over, and adherent to, the leaf. After a short distance, each strand expands into a small, fan-shaped, byssoid patch, as shown in the figure. Each of these patches then becomes a centre from which new strands radiate outwards, and this is repeated until a great part of the surface of the leaf is covered. Meanwhile, the strands first formed give off hyphae laterally, which intermingle so that a continuous sheet of interwoven hyphae is formed, the original pattern still being evident on a close examination. The colour of the fungus is dark brown or rufous-brown. Its hyphae are similar in colour, shape, and mode of branching to those of *Peziotrichum Lachnella*, but it lacks setae, and its globose bodies are not so distinctly stalked. No fructification has been observed in this species, but it is most probable that it is a *Septobasidium*, and that the globose bodies are probasidia.

Again, similar globose bodies occur in the basal layer of *Septobasidium suffultum* (B. & Br.) Pat. This species overruns scale insects on living twigs, covering the twig, in the early stages of development of the fungus, with a thin, rufous-brown byssoid layer, which is interrupted here and there by circular or oval gaps, each surrounded by erect setae. These gaps sometimes, but not invariably, mark the position of one of the host insects. The setae coalesce into fascicles, but these are not rigid, like those of *Peziotrichum Lachnella*. The repent hyphae of the basal layer bear globose, spore-like bodies, 12–16 μ diameter, which differ from those of *Peziotrichum Lachnella* in being uniformly thick-walled and apparently permanently hyaline. These are probably probasidia.

It seemed probable, from a comparison with the foregoing examples, that *Peziotrichum Lachnella* was a state of a *Septobasidium*, and that the globose bodies represented probasidia, although up to the present no species of *Septobasidium* to which

it could be referred has been found in Ceylon. But it differs from species of *Septobasidium* in its habit. In general, a *Septobasidium* grows uniformly in a continuous sheet over a colony of scale insects, or if it originates at several points in the colony, the separate growths coalesce. But in all the available specimens of *Peziotrichum Lachnella*, each individual insect bears its own small stroma, *i.e.* each insect is attacked separately, and there is no evidence of any fusion of the stromata by the outward growth of the hyphae over the leaf. This difference of habit would not necessarily exclude the fungus from *Septobasidium*, as there is no reason why reduced species of *Septobasidium* should not exist, in which each fructification might be confined to a single insect, as is the rule with *Aschersonia*.

Examination of other collections, however, has demonstrated that *Peziotrichum Lachnella* is a sterile stroma of an *Ophionectria*.

Ophionectria coccorum Petch.

This species was first collected by Mr E. E. Green in 1910, on *Fiorinia juniperi* Green on *Juniperus bermudiana* in the Botanic Gardens, Peradeniya, and has since been found repeatedly on the same group of trees. The insect is usually concealed under a scale leaf, and the fungus spreads from it over the adjacent leaves.

The perithecia are clustered on a dark brown, byssoid stroma, up to 1·5 mm. long, and 1 mm. broad (Plate VIII, fig. 6). The part of the stroma which overlies the insect consists of contorted hyphae, interwoven into a compact continuous mass, from which more regular hyphae spread out over the leaf and form a byssoid film. The latter hyphae are dark brown, rather thin-walled, septate, straight, 5 μ diameter, branching at an acute angle, the branches being straight, or occasionally flexuose (Plate VIII, fig. 7).

The perithecia occur in groups of up to about six, closely congregated but not adherent. They are conoid, up to 0·2 mm. diameter, dark brown, almost black when dry, but subtranslucent when moist, pruinose, with a thick parenchymatous wall. The asci are clavate, up to 100 × 8 μ, shortly pedicellate, moderately thick-walled, not capitate, and without an apical pore. The mature asci are distinctly green. The paraphyses are stout, 2 μ diameter, branched above, and slightly inflated at the apex. The asci (Plate VIII, fig. 8) are eight-spored, the spores being arranged in a parallel bundle. The ascospores (Plate VIII, fig. 9) are hyaline, linear, tapering slightly at the ends, almost as long as the ascus, 1·5–2 μ diameter, multiseptate.

This is an *Ophionectria* in the original sense. It differs from *Podonectria* in the shape of the ascospores.

From the same stroma there arise numerous erect setae (Plate VIII, fig. 10), up to 1·5 mm. high, which adhere laterally and form terete or conical fascicles. These usually arise near the perithecia. The separate setae are blackish brown, septate, up to 8 μ diameter, with a slightly inflated, hyaline apex, and closely resemble those of *Peziotrichum Lachnella*. The whole stroma with its setae resembles that of the latter species, but examinations of numerous collections from *Juniperus* at Peradeniya failed to show any globose bodies on the repent hyphae.

In 1924, specimens were collected on a scale insect on *Eugenia* at Bandaragama in the low-country of Ceylon. The stromata were well developed, and formed small mats up to 5 mm. diameter, each overlying a scale, the setae being situated in the centre of the stroma. The repent hyphae of the stroma bore globose bodies laterally and the fungus was typical *Peziotrichum*. Some stromata, however, bore perithecia of the *Ophionectria* in addition, and thus established the connection between the supposedly different fungi. The perithecia were usually situated at some distance from the setae; they agree completely with the perithecia of the Peradeniya collections. The majority of the stromata were barren, *i.e.* were *Peziotrichum Lachnella*. Only a few bore *Ophionectria* perithecia.

Attempts to get this species into culture have failed. Ripe ascospores are not frequently met with, but mature, extruded ascospores have been obtained by detaching the stromata from the leaf, placing them on a glass slip in a damp chamber, and supporting a cover glass over them. The extrusion of the ascospores, however, has not been observed to occur in a short time, and consequently many other fungi have an opportunity of developing before they are obtained. This usually happens with the present species, as numerous foreign spores are entangled in the byssoid stroma and the fascicles of setae. Hence mixtures of spores are found on the cover glasses, and it has not been possible to obtain pure cultures. The germination of the ascospores has not been observed. Failure has also attended attempts to obtain material for cultures by dissecting out the contents of the perithecium.

Ophionectria coccorum Petch, n. sp.

Perithecia gregarious, on a byssoid stroma, conoid, about 0·2 mm. diameter, dark brown, pruinose; wall thick, parenchymatous. Asci clavate, shortly pedicellate, thick-walled, up to 100 × 8 μ, eight-spored, the spores in a parallel bundle. Paraphyses stout, 2 μ diameter, branched, slightly inflated at the apex. Spores linear, straight or flexuose, 1·5–2 μ diameter,

nearly as long as the ascus, tapering slightly at the ends, multiseptate, with septa about 6 μ apart.

On *Fiorinia juniperi* on *Juniperus bermudiana*, Peradeniya, Ceylon.

Volutella epicoccum Petch.

Another fungus, which, macroscopically, bears a striking resemblance to *Peziotrichum Lachnella*, has been found at Hakgala (5600 ft.), on a scale (? *Lecanium*) on *Cinnamomum ovalifolium* Wight. It has been collected in that locality on several occasions during the last three years, but only on one tree.

The fungus covers the insect with a compact, plectenchymatous tissue and spreads out in a byssoid film over the leaf, forming a rufous-brown stroma, up to 2 mm. in diameter (Plate VIII, fig. 11). The part of the stroma which overlies the insect is thicker and denser than in *Peziotrichum*, and it is only possible to determine that the fungus is parasitic on an insect by teasing out the tissue and finding the remains of the scale.

At the margin of the thicker part of the stroma, there arise erect setae, up to 1·5 mm. high, which cohere laterally into rigid fascicles. These fascicles are arranged in a ring, as in *Peziotrichum*. The setae and the hyphae of the stroma are similar to those of *Peziotrichum Lachnella* and *Ophionectria coccorum*, but there are no globose bodies on the repent hyphae.

Rounded pulvinate masses occur within the ring of setae. They occur at the base of a group of setae, or in some instances are partly surrounded by setae which cohere above so that the pulvinate mass is enclosed within the base of a fascicle. These masses do not entirely cover the space within the ring, but two or three, clustered or solitary, are situated at its margin, in contact with the setae or partly encircled by them. Plate VIII, fig. 12, shows one of these masses separated from the rest of the fungus.

These pulvinate masses are sporodochia. When dry they are brownish, but white when moist. They are composed of closely-packed vertical conidiophores, brownish at the base, hyaline and branched above. The conidia are hyaline, cylindric, usually curved at one end, sometimes straight, attenuated at the curved end, obtuse at the other, 40–56 × 3 μ, continuous (Plate VIII, fig. 14).

Other specimens of this species have been collected on *Parlatoria aonidiformis* on *Cullenia excelsa*, at Ratnapura in the low-country of Ceylon, and these show a further development. The stroma grows over the insect, as in the Hakgala collections, in a dark brown disc about 1 mm. in diameter, with a margin of rufous-brown radiating hyphae. Some stromata

bear erect fascicles of hyphae, with pulvinate sporodochia at their bases, as in the specimens on *Cinnamomum*, but, in general, a single column arises from the centre of the stroma (Plate VIII, fig. 13). This column is up to 3 mm. high, and consists of a brownish black stalk, 0·75 mm. diameter below, expanding to 1 mm. diameter above, and terminating in a funnel-shaped head, up to 1·75 mm. diameter, bordered by triangular fascicles of dark brown hyphae, up to 0·4 mm. long. The stalk is smooth, sometimes with a few projecting bristles towards the base, and sometimes with a ring of setae, at a varying height, as though it had grown through a previously formed head lower down. It is composed of parallel hyphae, similar to those of the fascicles of setae in the other collections.

The inner hyphae of the stalk terminate as conidiophores, while the outer form a sheath round the head and extend above it in erect fascicles.

The mass of conidiophores and conidia is white when moist, and both are similar to those of the specimens on *Cinnamomum*, the conidia being somewhat longer, 48–68 × 2·5–3 μ.

No globose "conidia" occur on the basal mycelium.

In the occurrence of both sessile sporodochia and stalked synnemata, this species affords a parallel to *Microcera coccophila*.

The genus *Volutella* includes both sessile and stalked forms. The present species differs from *Volutella* in having a superficial stroma, but that is a consequence of its growth on a scale insect. It also differs from *Volutella* in having the setae adherent in fascicles, and, in its sessile form, in that they are adjacent to, rather than part of, the sporodochium.

Volutella epicoccum Petch, n. sp.

Stroma byssoid, up to 2 mm. diameter, bearing either sporodochia or synnemata. Sporodochia pulvinate, brown when dry, white when moist, accompanied by dark brown setae, up to 2 mm. high, 4–8 μ diameter, coalescent in fascicles. Synnemata terete, up to 3 mm. high, 0·75 mm. diameter below, 1 mm. diameter above, terminating in a funnel-shaped head, 1·75 mm. diameter, the outer sheath produced in elongated teeth, 0·4 mm. long. Conidiophores hyaline, stout, branched. Conidia terminal, solitary, hyaline, linear or narrow-clavate, straight or curved at one end, attenuated at the curved end, obtuse at the other, continuous, 40–68 × 2·5–3 μ. On scale insects, *Parlatoria aonidiformis* and ? *Lecanium* sp.

Attempts to germinate the conidia have been unsuccessful, and it has not been possible to get this species into culture. The general structure of the fungus strongly suggests a relation-

ship to *Ophionectria coccorum*. But, although both species have been collected on numerous occasions, no conidial stage has been found with *Ophionectria coccorum*, and no perithecial stage with *Volutella epicoccum*.

Volutella epicoccum has been collected at Hakgala (5600 ft.) and in the wet low-country, and in neither locality have pseudoconidia been found on the mycelium. *Peziotrichum Lachnella* has been collected at Peradeniya (1600 ft.), Bandaragama (sea level in the wet low-country), and Elephant Pass (sea level in the dry zone); it has pseudoconidia but no true spores. *Ophionectria coccorum* has been collected repeatedly on two contiguous trees at Peradeniya (1600 ft.), but all the collections from this locality lack pseudoconidia; it has also been collected sparingly at Bandaragama (wet low-country) in company with *Peziotrichum*, its stromata in that collection bearing pseudoconidia. Assuming that *Volutella epicoccum* is related to *Ophionectria coccorum*, the data suggest that, in general, pseudoconidia are only produced in the absence of conidia or perithecia.

EXPLANATION OF PLATE VIII.

Fig. 1. *Peziotrichum Lachnella*, Ceylon specimen, entire stroma. × 10.
Fig. 2. *P. Lachnella*, Ceylon specimen, repent hypha with globose bodies. × 300.
Fig. 3. *P. Lachnella*, enlarged figure of entire stroma, after Saccardo. Magnification not stated.
Fig. 4. *P. Lachnella*, enlarged figure of the setae and repent hyphae, after Saccardo. Magnification not stated.
Fig. 5. Setae of *P. Lachnella*, Ceylon specimen. × 300.
Fig. 6. *Ophionectria coccorum* on scale on *Juniperus*, entire stroma. × 20.
Fig. 7. Repent hyphae of *O. coccorum*. × 300.
Fig. 8. Ascus of *O. coccorum*. × 600.
Fig. 9. Ascopore of *O. coccorum*. × 600.
Fig. 10. Seta of *O. coccorum*. × 300.
Fig. 11. *Volutella epicoccum*, entire stroma. × 20.
Fig. 12. *V. epicoccum*, part of stroma with a single sporodochium. × 20.
Fig. 13. *V. epicoccum*, stalked form. × 20.
Fig. 14. *V. epicoccum*, conidia. × 500.
Fig. 15. ? *Septobasidium*, on scale insect on *Calophyllum*. × 7.

THE SOREDIA OF PELTIGERA ERUMPENS WAIN. AND P. SCUTATA KBR.

By O. V. Darbishire.

(With Plates IX and X.)

Introduction.

The soredium, which is a reproductive organ of the complete lichen, consists of a group of algal gonidia surrounded by a layer of fungal hyphae. The soredia generally occur in well-limited areas which are known as soralia. Following Acharius, however,

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du Rietz defines a soredium ((15) p. 376) as a decorticate portion of a lichen in which numerous reproductive units have been formed by the excessive increase of the gonidia. Each reproductive unit consists of a small group of algal gonidia surrounded by a fungal sheath, and is called by him a soredial grain or propagulum. The soredium of Acharius and du Rietz therefore corresponds to our soral, a term first used by the author ((3) p. 320), though originally suggested by Reinke in conversation. The soredial grain or propagulum of du Rietz corresponds to our soredium. Schwendener used the term soredium in our sense many years ago, when referring to *Usnea* ((17) p. 130 and 131). The term soral has now been generally adopted. Quite recently Magnusson said: "I find it practical to keep the much-used and useful term soralia for the distinctly limited places where soredia develop" ((10) p. 13). The term soredium is also very generally used in the Schwendenerian sense.

The ascospore reproduces the fungus only and not the complete lichen. Hymenial gonidia reproduce the complete lichen, but their occurrence is very rare (21). The soredia in fact represent the only common lichen reproductive organ which contains both gonidia and fungus, though a lichen may be reproduced by the breaking-up of the thallus into smaller portions. It is also possible that isidia may act in a reproductive capacity if by chance they get separated from the metathallus on which they are borne. Reproduction, however, is clearly not the main function of the isidium and the thallus fragment. The soredia are the only true reproductive organs of the lichen consortium.

Very little is known of the method of origin of the single soredium. Rosendahl speaks of certain isidia-like outgrowths of *Parmelia verruculifera* Nyl. which break up more or less completely with the formation of soredia ((16) p. 426). The soredia of *Evernia furfuracea* var. *soralifera* Bitter ((2) p. 482), and *Parmelia farinacea* Bitter ((1) p. 177) originate in a similar manner. Schwendener mentions the breaking through of the cortex by the soredia of *Usnea barbata* ((17) pp. 137 and 138), *Evernia vulpina* ((17) p. 160), and other lichens. In a paper on the Pertusariaceae of Germany the author gave an account of the origin of the soralia in *Variolaria globulifera* and *V. amara* ((4) pp. 647 and 656). A mass of hyphae grows up from just above the substratum and by pressure upwards breaks through the cortex ((4) p. 647, figs. 24–26). In a later paper the author described the origin of the soralia of *Roccella fuciformis* (L.)DC. ((5) p. 22) where again the cortex is ruptured by the growth of internal hyphae. The most detailed recent account of the origin of the soredium is that by Moreau ((12) p. 328, figs. 10–13) of *Lobaria pulmonacea* Nyl. Hyphae belonging to the upper

portion of the gonidial layer grow out, whilst the gonidia themselves at first remain inactive. Small groups of gonidia are surrounded by hyphae and are pushed up towards the cortex. In this way the soredia are differentiated and by pressure break through the cortex, the cells of which in the meantime have died off.

Very little is known about the fate of the soredium after it has separated from the parent plant. The author described the growth of some free soredia of *Variolaria globulifera* which were kept under observation for eight months. They measured about 50–60μ in diameter at the beginning of the experiment, and had reached a diameter of about 520μ when the experiment had to be concluded. By that time the soredia appeared to have obtained a firm hold on the substratum of cork ((4) p. 658).

Tobler has carried out similar experiments on the germination of the soredia of *Cladonia glauca* Flk. and *Cl. squamosa* (Scop.) Hoffm. ((23) pp. 409–417, Pl. III, fig. 11). In a macro-culture he observed the formation of a primitive *Cladonia*-thallus by the coalescence, as he thought, of several separate soredia. Both Tobler's observations and my own merely show that the soredia are organs of reproduction. The details of the process of germination of the soredium and its subsequent growth to form even a primitive lichen thallus have not yet been recorded.

Schwendener described for *Usnea* what can only be called the germination of soredia *in situ*, that is in the tissue of the soral which has given rise to them. A single soredium may grow out and give rise to what he calls a soredial branch ((17) pp. 137–139; Pl. II, figs. 16, 18–20, 23–24). This can be distinguished from the ordinary or adventitious branch because the cortex of the latter is continuous with that of the main axis, which is not so with the soredial branches. A specimen of *Usnea* which bears numerous soredial branches is thus not a single organism but a multiplicity of individuals ((17) p. 139). Schwendener's soredial branches represent a very extraordinary example of a daughter organism becoming parasitic on the parent thallus. Kajanus makes use of the term "soredial branch" when writing of the isidia of *Peltigera rufescens*, a species which I should probably call *P. praetextata* ((8) p. 42), but Kajanus draws no sharp line between soredia and isidia.

Krabbe has discussed at some length the soredia of the genus *Cladonia*. He describes the growth of foreign *Cladonia* soredia which are blown on to the podetia of certain species of *Cladonia* and become fixed to this new substratum ((9) p. 118). The soredia thus blown on to any specimen of *Cladonia* may belong to almost any species of *Cladonia*. In the end only the algae are retained as gonidia by the fungus of the host. The original

fungal hyphae surrounding these gonidia degenerate and die off, so that only the algae are left over from the alien soredia ((9) pp. 126 and 127). It should be mentioned that Krabbe claimed that the upright thallus or podetium of *Cladonia* was entirely a fruit body, and as such, primarily at any rate, bore no gonidia. All the gonidia found on a podetium appear to have come from other specimens except a few which are derived from the gonidia of the protothallus which gave rise to the podetium ((9) p. 115). It is in view of the great importance of the soredium to the lichen, that I have studied in greater detail the soredia of two species of *Peltigera*, *P. erumpens* and *P. scutata*. These species of *Peltigera* were chosen because I had already investigated the isidia of *P. praetextata* ((7) p. 739).

It is not as yet possible to say what is the full systematic value of the soredium. It is doubtful whether all soredia are homologous structures, or even whether they are all analogous structures. There is no doubt, however, that the soredium of the lichen is polyphyletic in origin.

During an examination of the German species of the Pertusariaceae I laid stress on the presence or absence of soredia for systematic purposes ((4) p. 595), and re-established the genus *Variolaria* Ach. which included those species of *Pertusaria* DC. bearing soredia. There are other differences between these two genera which clearly indicate that, though allied, they should be kept separate, although this separation has not been accepted by lichenologists. To Bitter belongs the credit of having been the first to study carefully the systematic value of soredia. In the course of a systematic investigation of certain species of the sub-genus *Hypogymnia* of *Parmelia* ((1) p. 171 *et seq.*) he made special use of the development and morphology of the soralia for systematic purposes. The presence of soredia is in many cases clearly a definite feature characterising, and thereby separating, certain species, if this term is used in the conventional sense.

Peltigera erumpens and *P. scutata* always bear soredia. They are not merely sorediiferous forms or varieties of species of *Peltigera* which do not necessarily produce soredia. Du Rietz states this quite definitely ((14) p. 210) and I fully agree with him. Many lichenologists look upon sorediiferous individuals as mere biological or ecological forms or varieties and assume that certain conditions must be fulfilled before a species will bear soredia. But certain conditions too must be fulfilled before sorediiferous species like *P. erumpens* and *P. scutata* will grow at all. These two species are not on that account biological species: they are genotypes as regards the property of producing soredia. Moreau looks upon sorediiferous specimens of the genus *Peltigera* as being a more or less direct result of the influence of

the surrounding conditions; that is as being representatives of a species not necessarily bearing soredia ((11) p. 115). Kajanus, too, considers the occurrence of soredia and similar growths as a biological phenomenon depending on more or less accidental external conditions ((8) p. 42).

P. erumpens is recognised as a good species by A. Zahlbruckner ((25) no. 6235). Other lichenologists have looked upon it as a variety of *P. canina* Willd., of *P. rufescens* Hoffm., of *P. pusilla* L., or of *P. spuria* DC. *P. scutata* Kbr. also is recorded by A. Zahlbruckner as a separate species ((25) no. 6251), and this is the status assigned to it by most lichenologists to-day. The soralia of *P. erumpens* are circular in outline. In *P. scutata* they occur in marginal or superficial soralia which are long and narrow. In the British Museum Catalogue of British Lichens ((19) p. 92) *P. erumpens* Tayl. is listed as var. *erumpens* Hue of *P. canina* Willd. It is recorded from Dunkerron, County Kerry. I have found it near Thirlmere. *P. scutata* Kbr. is recorded in the same catalogue ((19) p. 94). It is a fairly common British species. Olivier records a forma *sorediata* of *P. rufescens* ((13) p. 158). Not having seen specimens of this form I cannot say whether it is really sorediiferous, but judging by his description of the variety *praetextata* of *P. rufescens* which he also refers to as sorediiferous, it is possible that he does not distinguish clearly between isidia and soredia. Sydow obviously does not separate soredia and isidia as he assigns the presence of marginal scales and soredia to the variety *praetextata* of *P. rufescens* ((22) p. 59), though *P. praetextata* never bears soredia, but isidia only. He also characterises the forma *crispata* of *P. canina* as possessing marginal soredia which again is incorrect. The structures found at the margin are either closely set lobes of the ordinary thallus or true isidia. In the latter case his f. *crispata* is a synonym for *P. praetextata*. A. Zahlbruckner seems to be of the same opinion though he places *P. praetextata* as a variety of *P. rufescens* ((25) no. 6249). Bitter finds that in *Parmelia farinacea* Bitter the isidia produce soredia at their tips. This process he suggests might be looked on as a transition from the isidial to the soredial formation. He is nevertheless of the opinion that isidia and soredia should be kept separate ((1) p. 177) and is therefore misquoted by Rosendahl who states that in Bitter's view no sharp line can be drawn between isidia and soredia ((16) p. 31), and Smith ((18) p. 143). I do not wish to pursue the matter further here, but will again refer to du Rietz who recognises as distinct sorediiferous species of *Peltigera* only the two species just mentioned, namely *P. erumpens* and *P. scutata*, just as he recognises only two isidiiferous species, in *P. praetextata* and *P. lepidophora* ((15) p. 382). He makes here

full use of isidium and soredium for systematic purposes and also draws a sharp line between isidium and soredium.

Methods.

The methods adopted in preparing the material for this paper were simple. Fixation was by absolute alcohol or weak Flemming. The microtome sections were cut in the usual way after passing the material through cedar wood oil and hard paraffin. Sections were stained with fuchsin and mounted in glycerine jelly.

The Structure of the Metathallus of *P. erumpens*. (Figs. 3 and 4.)

The structure of the metathallus of *P. erumpens* differs but little from that of *P. canina* ((6) p. 17, fig. 1). The thallus is on the whole less coarse and thick but the same tissues are found in both species.

The following measurements obtained for the various portions of the metathallus of *P. erumpens*, are here compared with those of *P. polydactyla* Hoffm. ((7) p. 731), which are given in brackets. The cortex of *P. erumpens*, 40 to 50 μ deep (30 to 40 μ in *P. polydactyla*), is made up of the usual vertical rows, composed of 2 to 3 (2 to 4) cylindrical cells with a diameter of 10 to 20 (5 to 18) μ. Each cell may be 10 to 24 (up to 24) μ or even 28 μ in height. The walls are of a uniform thickness of 2 (1·5 to 2) μ, the total wall substance separating two neighbouring cell cavities thus amounting to 4 (3 to 4) μ. Over a distance of 100 μ the cortex of *P. erumpens* has about 9 (10) cells, and is normally quite uninterrupted. The cortical cells of *P. erumpens* are characterised by their large size and uniform roundness, while those of *P. polydactyla* are more angular. The actual surface of the cortex of *P. erumpens* is uneven, though not actually rough or scabrid.

The gonidial layer is 60 to 80 (60 to 80) μ deep, and consists of short threads of *Nostoc* cells measuring about 4 to 8 (4 to 10) μ in diameter and embedded in a clear mucilage to a depth of about 1 to 2 (2 to 3) μ. The intergonidial hyphae are delicate, measuring 2 to 4 (5 to 6) μ in diameter, and finer branches sometimes actually enter the gonidial mucilage. Air spaces are found separating the intergonidial hyphae. The *Nostoc* groups are closely surrounded by the intergonidial hyphae, though in the lowest portions of the gonidial layer the mucilage is often quite free of any hyphae, thus becoming fully exposed to the air circulating inside the metathallus. Hyphae run from the cortex right through to the hypothallus, though they are not so frequent as in *P. polydactyla*.

The medullary hyphae can be divided into infra-gonidial hyphae, the measurements of which vary very much, their diameter being on the average about 6 (4 to 6) μ, and the special conducting hyphae which run in well-developed strands up to 40μ in thickness. The separate hyphae have a diameter of about 16 (8 to 10) μ. The hypothallus is not on the whole very well marked and it varies very much in depth, which does not exceed 20 (80 to 100) μ. The separate hyphae measure 6 (5 to 6) μ in diameter, of which a total of 4 (4) μ is due to the two walls. The total thickness of the thallus of *P. erumpens* does not exceed at the most 0·4 mm., while usually it is uniformly 0·35 mm. thick (0·5 to 0·55 mm.).

The rhizines, generally short and very thin, do not exhibit the clear differentiation between inner conducting hyphae and outer hypothallus-like hyphae which we find in *P. praetextata* and other species of *Peltigera*. In *P. erumpens* all the hyphae of the rhizine run in a more or less longitudinal direction. The hyphae of the metathallus bend out into the rhizine just as they do in the larger species, that is in such a way that they cross over to the opposite side of the rhizine before taking a strictly longitudinal direction. The rhizine is about 70 to 80μ in diameter, a single central hypha measuring 10μ across, while the wall is about 3μ thick. At the periphery of the rhizine the hyphae, which are still running in a longitudinal direction, measure 5 to 6μ across, with walls whose thickness is 2μ. The hyphae are firmly cemented together and cross-pieces or struts can be seen, though they are far rarer than in *P. praetextata*, *P. canina* and others. The inbending of the free apex of the rhizinal hyphae to form the struts is rarely observable ((7) p. 734). The hyphae of the rhizines of *P. erumpens* probably spread out in the sandy or loose soil and possibly absorb water more by the functioning of the thick walls than by the working of numerous intercellular air spaces which are less extensive than in other species. *P. erumpens* does not form big strong rhizines, which are so characteristic of the larger species.

Cracks, so-called, occur in the cortex of *P. erumpens*, though they appear to be rare. I have seen them in a few instances but they had all been healed over. Hyphae had grown up from the infra-gonidial layers and the wound was completely closed by a continuous covering extending from cortex to cortex. In one specimen, gonidia were gradually filling up the gap in the gonidial layer by an extension from the neighbouring portions of the layer. The breadth of this scar, which measured 0·35 mm. across, seemed to indicate that the break in the cortex had been brought about by the attacks of some small marauding animal, rather than by some mechanical agent, as so commonly occurs

in other species of *Peltigera*. I have referred to the wound and its healing over in order to point out that a break in the cortex does not necessarily lead to the formation of soredia.

The Soredia of *P. erumpens*.

Soralia occur in *P. erumpens* in the form of circular interruptions of the cortex (Fig. 1). They are of a lighter colour than the metathallus. The smallest soralia are found nearer the margin and the largest and oldest nearer the centre of the thallus. It is clear that the soralia originate near the margin. In this region very closely interwoven hyphae which are branches from the longitudinal medullary hyphae may be noticed here and there in the inter-gonidial and infra-gonidial layers. Air spaces are almost absent from this tissue at this time. The few hyphae of the future soral grow upwards towards the cortex and push their way into it, thereby making a break in the continuity of the primary cortex (Fig. 3). No open wound is formed by which the underlying tissues become exposed. All the evidence I have collected points to the fact that the initial hyphae of the soral themselves cause the break in the cortex rather than that the continuity in the cortex is interrupted by external mechanical means.

The initial hyphae can be readily distinguished from the ordinary cortical cells, as the latter are larger and the regular course of the single cell row is often lost. In the initial soralial hyphae which have forced their way into the old cortex the course of the cell rows can be made out very clearly (Fig. 3). It appears that the function of the soralial hyphae is to interrupt the continuity of the old cortex in order to allow the main tissue of the soral to come to the surface (Fig. 4). The real break in the cortex therefore occurs between the group of initial hyphae and the old cortex. These two tissues are then separated by the new main tissues of the soral. The actual break in the cortical continuity and the initial hyphae can be clearly seen on the sides of the growing mass of main soralial tissue. In later stages the initial hyphae can usually no longer be distinguished (Fig. 2). Whether the main soralial tissue forces its way in between the initial hyphae and cortex or whether owing to growth the formation of a gap is threatened, into which the soralial tissue grows, has not been clearly made out. It is very likely that both conditions co-operate. In any case no open wound is formed (Fig. 4).

The main soralial tissue consists of branched hyphae which are based on the infra-gonidial longitudinal medullary hyphae, and run mainly towards the cortex, forming a very close plectenchyma (Fig. 4). Air spaces are few, except near the

lower ends of these hyphae where they arise from the infragonidial layers. The outer covering cells form a continuous layer which acts as a protection for the underlying gonidia.

The activity of this main soralial tissue is almost the same in the young and in the old soral where it forms a more or less continuous, though often uneven, layer over the whole soral. In quite old soralia, the continuity of this actively growing layer may be interrupted but never in such a way as to expose the gonidia to the possibility of desiccation (Fig. 2). It is impossible to say at which point the separate hyphae of the growing soralial tissue are most actively dividing. The cells, on the whole, are short, and new cell formation therefore in all probability proceeds along the whole length of each hypha.

The following is the course of development of a single soredium and of its gradual differentiation into a separate unit from the general tissue of the soral (Figs. 4 and 5). Branches arise from the medullary hyphae and grow in between the lower groups of gonidia. At this point these groups are round or oval in shape, and generally are partly exposed to the air, like all the lower gonidial groups in the metathallus (Figs. 4 and 5). The branches of the medullary hyphae grow so as to separate the groups of algae which lie close together and to surround these smaller groups by a continuous fungal sheath. Larger groups apparently may be broken up. The hyphae at first run in various directions (Fig. 5), but gradually straighten themselves out as they grow towards the upper surface of the soral (Fig. 5). The gonidial groups also alter their shape in conformity with the straightening of the hyphae. The gonidial groups become elongated as they move along with the hyphae. The algae must be growing actively as their groups consist of more cells as they approach the upper surface of the soral. Air spaces are few in this part of the soral and are probably very small, so that they are generally overlooked.

Near the surface of the soralial tissue the soredia now begin to be differentiated, the first indication of the coming differentiation being visible on the actual surface (Fig. 5). A slight projection is formed immediately above the group of algae which is going to form the gonidial element of the soredium. The projection becomes more distinct, and from being only a few cells broad it gradually becomes bigger. At first the projection with its underlying gonidial groups is very much longer than broad and becomes more rounded as it separates from the main mass of the soralial tissue. In conformity with this change in position of its surrounding hyphae each gonidial group assumes a more rounded shape. Gradually the little mass of tissue which was capped by the projection becomes almost freed from the main

tissue as it is pushed up by a number of single hyphae (Figs. 6 and 7). It is by these single hyphae that the now almost completely separated soredium remains in touch with the parent plant. Laterally the soredium may be in close touch with its neighbouring sister soredia but there is no actual connection between them. The cells of the lower hyphae which form what we might term the stalk of the soredium grow in width and length and are evidently pushing the soredium up. These cells gradually assume a barrel shape and by a split in the transverse walls the soredium is ultimately completely separated from its parent plant. During the last stages the gonidia have become more active and even the smallest free soredium contains several groups of gonidia and air spaces begin to make their appearance owing to the growth in length of the internal hyphae (Fig. 8). The outer layers of the soredium act as a protection for the gonidia and they appear at first, at any rate, to be continuous (Figs. 6 and 7). In the irregularly outlined cortex so formed pores are later found by which the outside air can communicate with the air in the rapidly growing air spaces inside the soredium (Figs. 8–10). These pores are formed either by the separation of the cell walls or by the want of coalescence when new hyphae are interpolated between older cells, similar to the method of origin of the pores on the underside of the isidia of *P. praetextata* ((7) p. 746).

The gradual separating out of the single soredium from the general undifferentiated soralial tissue cannot always be followed out in the way which has just been described. Gonidial activity on the whole keeps pace with hyphal activity—and therefore all stages are found in the differentiation of the soredia from below upwards (Fig. 5). It would appear, however, that gradually all the gonidia at one point are used up in the formation of soredia as one group of gonidia after another has been dealt with basipetally. Hyphal activity may thus in the end exceed gonidial activity so that no gonidia are left at that point (Fig. 2). When this occurs, it is almost certain that, in due course, the gonidia spread to this spot again.

A mature soredium is more flattened in a vertical direction than is a young one, and it shows the following structure (Fig. 8). It is completely surrounded by a cortex, the cells of which clearly show their hyphal origin by being elongate. Their outline is often very uneven and is interrupted here and there by very small pores (Figs. 9 and 10). A clear differentiation of the internal tissue characterises the mature soredium. The gonidial groups have increased in number and fill the inside of the soredium closely. Numerous narrow inter-gonidial hyphae penetrate into the folds of the mucilage of the gonidial groups,

though they no longer completely surround them. Extensive air spaces have again made their appearance and are often directly bordered by the mucilage enclosing the gonidia. In the mature soredium we thus get a primary cortex and gonidial groups which are well rounded off and closely in touch with the intergonidial hyphae. Though the soredia may be slightly flattened it is not possible structurally to differentiate between an upper and lower side.

A mature soral may give a wrong impression as to its origin (Fig. 2). The margin of a soral is made by the abrupt ending of the original cortex of the metathallus. This cortical layer is often thrown back, making it appear as if the soralial tissue had originally burst through the cortex in an irregular way, and so rolling it back as fresh portions of the gonidial layer were broken up into soredia. This, however, is not generally the case. The exposed surface of the soral increases, not by the cortex being continually rolled back, but by the growth of the underlying medullary hyphae and the cortical cells which surround the soral. The cortical margins of the soral are moving away from one another through the growth of the medullary hyphae. These grow in length and the cortical cells grow in diameter. This growth accounts for the extension of the soral. At the same time it is almost certain that the gonidia lying near the edge of the soral but still under the cortex are to a limited extent made use of as material for the differentiation of soredia, and in this way the cortex is rolled back to a limited extent (Fig. 2).

In cultures of *P. erumpens* which had been kept going for more than a year the greater part of the original lichen had apparently died. At its margin it had given rise to small regenerative nodules which seem to occur only in culture and under artificial conditions. I have found these nodules in other species of *Peltigera* which have been kept in cultures under similar conditions. In the culture of *P. erumpens* I found after nine months a number of small soredium-like bodies on the small moss plants over which the original *P. erumpens* plants had been growing. By the end of fourteen months some of these bodies had grown up into small thalli, one of which measured about 2 mm. in length and was about 0·5 mm. broad. At the same time quite small green bodies were found growing on neighbouring moss plants and these appeared to be soredia which must have come from *P. erumpens*. When examined under the microscope one measured about 0·5 mm. across and it was about 0·2 mm. thick. From one point on the underside arose a bundle of hyphae which had grown out to a distance of about 1·3 mm. (Fig. 11). The hyphae exhibited the usual apical

fusions which are characteristic of the growth of the free medullary and rhizinal hyphae of all species of *Peltigera* ((7) p. 734, fig. 10) I have examined. This specimen still possessed a continuous cortex which by the arrangement of its cells recalled the structure of a typical soredium of *P. erumpens*, and circumstantial evidence is strongly in favour of its being so. It has not, however, been possible to observe how the little differentiated soredium passes through the later stages after germination into the much more highly differentiated thallus of *P. erumpens*.

Structure of *P. scutata*.

In structure *P. scutata* resembles *P. erumpens* but the gonidial layer of the latter varies in depth only from 60 to 80μ, whereas that of the former varies from 40 to 100μ. This variation in the depth of the gonidial layer of the metathallus is a very noticeable feature of *P. scutata*. The algal groups are frequently not completely surrounded by fungal hyphae. The medullary hyphae are loosely interwoven and reach a thickness of 4 to 20μ, thus exceeding in diameter those of *P. erumpens*. The most characteristic structure by which we can separate *P. erumpens* from *P. scutata* is found in the light-coloured veins of the former which are very prominent especially after the thallus has been moistened, whereas *P. scutata* has veins which are dark in colour and which, though clearly distinguishable in surface view, are not prominent, while between the veins are the usual lighter-coloured cyphellar gaps. The metathallus of *P. scutata* is on the whole thicker than that of *P. erumpens* the difference amounting to about 0·1 to 0·2 mm. The dark rhizines of *P. scutata* show the internal differentiation which is found in *P. praetextata* whereas the rhizines of *P. erumpens* are light-coloured, and simple in structure. Speerschneider was the first to give an account of the anatomy of *P. scutata* (20).

The Soredia of *P. scutata*.

The soredia of *P. scutata* occur in two kinds of places on the thallus (Figs. 12 and 13). When the protothallus ceases to grow, it may give rise to soredia. This puts an end to further extension of the thallus and the lateral edges of most of these thalline lobes bear soredia. These form a soral which laterally has no bounds. Occasionally the actual growing margin may give rise to soredia. Soredia also occur on the surface of the thallus in long narrow breaks in the cortex which can be called soralia with rather more justification. In both kinds of soralia the original soralial hyphae arise from infra-gonidial or medullary hyphae.

It is difficult to point to any special feature in the method of origin of the marginal soredia. When the condition is established which results in the formation of soredia, the infra-gonidial and upper medullary hyphae become active. The algal groups are closely surrounded by fungal hyphae and small single groups are separated off from the general gonidial layer and are pushed towards the margin as separate soredia. The medullary layer thus becomes very active, but no fresh cortex is formed. As a result the older cortex is thrown back and the soredia are raised to above the level of the old cortex. The actual area of cortical surface is not much reduced thereby, as the soredia are pushed up from just below the cortex without probably any cortical cells being removed. The cortex is a layer which, even near the margin, soon loses its power of growth by the formation of new cells, so that it would be of little use to an actively reproductive organ like a soredium.

The soredia of the superficial crack-like soralia originate in the same way as the circular soralia of *P. erumpens*. Once however the continuity of the cortex has been interrupted the tissue of the soral becomes very loose. The two edges of the crack now act very much in the same way as the margin of the thallus does when it gives rise to soredia. Each margin of the crack is thrown back and the active soredia-forming hyphae push up detached groups of gonidia. These hyphae run at right angles to the general direction of the medullary hyphae and parallel to the soralial edges which stand upright on the surface of the metathallus.

The soredia of the superficial soralia do not differ structurally from those of the marginal soralia. In both cases the few algal gonidia are surrounded by the fungal sheath and the extent of the air spaces is limited. The outer layers are irregular in outline, but appear at first, at any rate, to be uninterrupted by pores. The several soredia gradually move upwards and this movement is due to the growth in length of the soralial hyphae. The whole soralial tissue is much looser in *P. scutata* than in *P. erumpens*, at the same time it is possible to see that the gradual differentiation of the soredium takes place in much the same way. A small round group of gonidia, closely surrounded by hyphae, moves towards the edge of the crack of the thallus margin, becoming slightly drawn out during the process. Then as the soredium becomes more differentiated, the group of algae again becomes rounded and gradually the soredium separates from the neighbouring cells and is free to be carried away. The superficial soralia always remain narrow which is due to the facts that the underlying medullary hyphae do not grow very much in length and that the cortical cells only increase in diameter slightly.

Experiments with the germination of soredia of *P. scutata* have so far been unsuccessful but they are still in progress.

Discussion.

Reference was made to the origin of the soralia in the introductory remarks to this paper. The general impression one gains from a study of the literature is that the cortex is ruptured or broken through by pressure from within. This is the view expressed by Schwendener (17), Bitter (1, 2), Moreau (12), Rosendahl (16), myself (5), and many others; while others consider the pressure from within to be due to conditions favouring increased activity of the gonidia.

There is, however, no real tearing through of the cortex in the case described in this paper. Regular hyphae which are of infra-gonidial medullary origin make their way into this layer, and cause the cortical cells to separate without thereby creating an open wound. The true soralial tissue subsequently enters this gap in such a way that the underlying gonidia never become exposed. No portion of the cortex is destroyed. The infra-gonidial hyphae of the medulla apparently remain potentially meristematic throughout the life of the lichen. It is difficult to say to what stimulus the soral owes its origin. It can safely be stated that the stimulus affects both gonidia and fungus. That is why the result is always exactly the same. It is *not*, however, possible to say whether the stimulus causing the formation of the soralia affects the gonidia or the fungus first. There is no evidence to show that the algae play a predominant part in this process. The algae are never normally seen to get ahead of the fungus. The separation and differentiation of the soredium does not begin till the group of algae forming its gonidia has been completely surrounded by hyphae. Algae and fungus are clearly co-operating closely during the formation of the soredium.

I do not consider that moisture or drought are direct causes of soral formation. The hyphae which closely surround the gonidia have walls which act in the same way as the walls of the hyphae forming the cyphellar tissue. They will not moisten with water, so the soredia at first sight appear dry. In the soredia we have a state of the lichen in which it can pass through very dry conditions, as is usual with reproductive organs.

The production of soredia may be due to the ageing of that particular portion of the thallus. This impression might be gained from the position of the marginal soredia in those parts of the thallus of *P. scutata* which are no longer actively growing,

though this would hardly hold good for the superficial soralia of *P. erumpens*. On the other hand the formation of soredia may be due to an internal and otherwise unsatisfied reproductive stimulus ((6) p. 23), and thus bear some relation to the activity with which apothecia are formed on the same plant. I have discussed this question on former occasions (4, 5), and the views expressed by me have been criticised by Bitter ((1) p. 189 *et seq.*) and others.

Kajanus applies the term soredial branches to the isidia of *P. rufescens* (= *P. praetextata*). Reference to this is made in an earlier part of this paper. A soredium is an organ that becomes completely separated from its parent thallus. A soredial branch would therefore represent a soredium which has attached itself to its parent plant after having first become separated. That is apparently what happens in *Usnea barbata* as recorded by Schwendener ((17) pp. 137–139). It does not occur, however, in the isidia of *P. praetextata*. No separation of an isidium takes place ordinarily, but gonidial and infra-gonidial tissues grow up to form the isidium, the internal layers of which always preserve full continuity with the corresponding tissues of the parent metathallus ((7) fig. 36). The isidia of *P. praetextata* and the soredia of many lichens have in common only the fact of their endogenous origin as their subsequent development is quite different. It is still an open matter, I consider, whether the "soredial branches" of Schwendener are isidia pure and simple or not.

In this paper I am more directly concerned with showing how intimately algae and fungus work together. This intimacy is so great that any stimulus internal or external affecting one constituent of the lichen will also, if necessary, affect the other ((7) p. 754). That is why the structure of the soredium is so uniform, and it also accounts for the uniformity in the structure of the whole lichen.

It must never be forgotten that there is one great difference between the algal gonidia and the lichen fungus. The gonidia of an individual lichen may be descendants of a long line of algal ancestors which have never acted as gonidia in a lichen before. Except possibly in some of the very simplest lichens, the fungal constituent of the lichen is the descendant of a very long line of ancestors which have for untold generations lived, and which now can only exist, in partnership with algae. The lichen tradition is passed on from lichen individual to lichen individual only through the mechanism of heredity of the fungus. The algal cells will often be quite unused to the lichen partnership. Even, however, when in the soredium gonidia which are related by descent are handed down from one vegetative genera-

tion to another, they have not acquired any lichen traditions. These are transmitted by the lichen fungus only. This shows what an important part the fungus must play in lichen morphology and physiology. It does not, however, mean that the fungus is a predominant partner in the lichen consortium. Fungus and algae are as closely associated in the lichen as green and colourless tissue in the green leaf of an oak tree ((7) p. 753), and they are as dependent on one another.

The fungus has lost the power to live other than in association with the algae. Has it acquired any really new traditions? I think it can be suggested at least that it has learnt to respond immediately to any condition affecting the welfare of the gonidia. It will not grow up into a lichen without the presence of algae which stimulate it to do so.

The ascospore of the fungus reproduces on germination the fungus only. Yet the nucleus, if it is the carrier of inherited characters at all, must bring with it all the special lichen-genes. If the formation of soredia is due to some special inherited factor or set of factors, these must be transmitted from generation to generation by the ascospore or any vegetative reproductive organ of the fungus. So that it should be quite possible, should sexual reproduction take place in lichens, to produce hybrid lichens even if the algae remain the same.

In the introduction to this paper reference was made to the manner in which some authors failed to distinguish isidia from soredia. As regards function isidia are mainly assimilatory organs, that is they are vegetative organs which normally remain attached to the parent plant. The soredia are reproductive organs which are shed by their parent plants, and are of endogenous origin. Isidia may be endogenous, but they may also be exogenous; this depends really on the method of cortical growth in the particular species. An isidium may produce soredia at its tip, but this does not imply that the isidium is passing into soredia. Isidia and soredia are both distinct lichen organs.

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Summary regarding the Soredia of *P. erumpens* and *P. scutata*.

1. In *P. erumpens* and *P. scutata* the superficial soralia originate endogenously by the activity of infra-gonidial hyphae which push their way into the cortex without actually tearing a gap or making an open wound. The marginal soralia of *P. scutata* are also of endogenous origin but the soredia are pushed past the cortex of the actual margin.

2. It is impossible to say whether gonidium or fungus initiates the soral.

3. Throughout the development of the soredium fungal hyphae surround the gonidia closely. When the separation of the soredium is complete air spaces make their appearance and gradually become extensive. These are found to be in touch with the outer air by pores in the protective layer.

4. The conditions which cause the formation of soredia must directly or indirectly affect both gonidia and fungus; these therefore co-operate perfectly during the development and growth of the soredia.

5. Soredia and isidia differ from one another in that the former become completely separated from the parent metathallus while, except accidentally, the isidia remain permanently in connection with their parent plants.

6. The soredia are reproductive organs; the isidia act as assimilators.

7. Of the two lichen constituents the fungus is the lichen habitual, the gonidium the lichen casual. The fungus has learnt to interpret the wants of the algal gonidia perfectly. The gonidium has learnt nothing, yet, as a system, the lichen form of symbiosis works perfectly.

8. The infra-gonidial hyphae remain potentially meristematic throughout the life of the lichen.

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EXPLANATION OF PLATES IX AND X.

Fig. 1. *P. erumpens*. Habit of plant showing prominent veins, rhizines, and circular soralia. The material for this figure was collected by Fuehrer at Gumbinnen in August 1924. ×4.
Fig. 2. *P. erumpens*. Vertical section of well-developed soral. The cortex has been rolled back at the edges of the soral. ×50.
Fig. 3. *P. erumpens*. A group of hyphae of infra-gonidial origin have pushed their way in between the older cells of the cortex, thereby making a break in the continuity of the cortex. ×300.
Fig. 4. *P. erumpens*. Vertical section of young undifferentiated soral. On the left are seen the group of hyphae referred to in Fig. 3. On the right is seen the break in the cortex. In the centre the true soralial tissue has grown into the gap formed by the initial hyphae. The continuity of the covering layers should be noted. ×300.
Fig. 5. *P. erumpens*. Vertical section of active soralial tissue in which the gradual separation of the soredia can be followed out. Below, the roundish gonidial groups are being surrounded by hyphae. These groups gradually get drawn out as the soredia become differentiated. The upper edge shows three slight projections, the beginnings of as many soredia. Quite on the top is the lower portion of an almost free soredium. ×800.
Fig. 6. *P. erumpens*. A single soredium being pushed up by hyphae from below. There is an almost complete absence of air spaces inside. On the left is seen the edge of the cortex of the margin of the soral. ×800.
Fig. 7. *P. erumpens*. A soredium in a slightly freer condition. It is attached by only one hypha to the general soralial tissue. ×800.

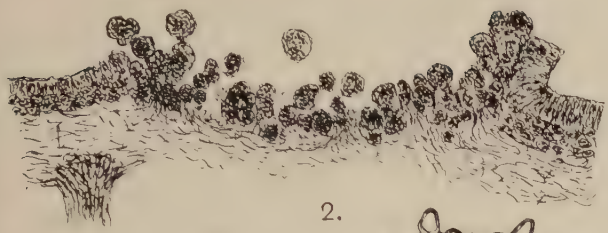
Fig. 8. *P. erumpens.* A mature quite free soredium found lying on a portion of the metathallus adjacent to a soral. The now extensive air spaces are indicated by thick lines. The intergonidial hyphae have grown, and so have the outer cells, and the gonidia. Pores are seen in section. × 800.
Fig. 9. *P. erumpens.* Pore of mature soredium seen in section. × 800.
Fig. 10. *P. erumpens.* Pore of mature soredium seen in surface view. × 800.
Fig. 11. *P. erumpens.* Two outer cells of a germinating soredium (probably belonging to *P. erumpens*) which have sent out a hypha each, which have become joined by a strut. × 800.
Fig. 12. *P. scutata.* Habit of plant showing marginal and superficial soralia. The material for this figure was collected by Dr du Rietz at Uppsala in May 1926. × 800.
Fig. 13. *P. scutata.* Vertical section of a marginal and a superficial soral. × 50.
Fig. 14. *P. scutata.* Single soredium near the edge of a superficial soral. It is being pushed up by one large hypha previous to becoming quite free from the general soralial tissue. × 800.

ON THE OCCURRENCE OF DIAPORTHE PERNICIOSA OR A CLOSELY RELATED FORM ON LILAC.

By F. C. Deighton.

In the course of an investigation at Cambridge during the last two years, of fungi occurring in the wood of lilac, a fungus hardly differing from *Diaporthe perniciosa* was very commonly isolated. It was found to be the most constant fungus isolated from the dead branches of several different bushes. Here it was generally associated with various other fungi such as *Fusarium*, but none of these was as constantly obtained as was the *Diaporthe*. Inoculation experiments were carried out on healthy lilacs with the *Diaporthe* and several of the other fungi isolated, but with no success. An account is given of some inoculations made with *Diaporthe perniciosa* and with the *Diaporthe* from lilac on peach and plum.

While on lilacs growing healthily in unshaded places no extensive die-backs occurred, it was found that on a lilac badly overshadowed by adjacent tall bushes, whole branches had died to the base, while most others were unhealthy. The appearance of some of the diseased branches was similar to that described by Miss Cayley (3) and Briton-Jones (1) for fruit trees affected with *Diaporthe perniciosa*. A slightly sunken area about an inch broad extended down one side of the branch. Behind it, the bark was dead and brown, and the wood discoloured to the centre, the discoloured portion appearing V-shaped in cross-section, very much like the photograph of *Diaporthe perniciosa* on cherry laurel in Briton-Jones's paper. The discoloured zone was always on the opposite side to a living branch, and was approximately the same breadth throughout its length.



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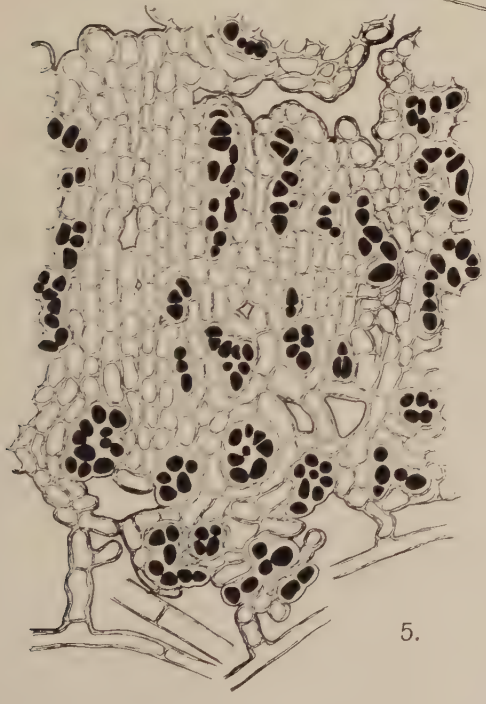

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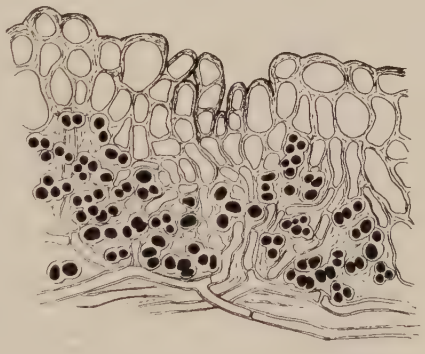

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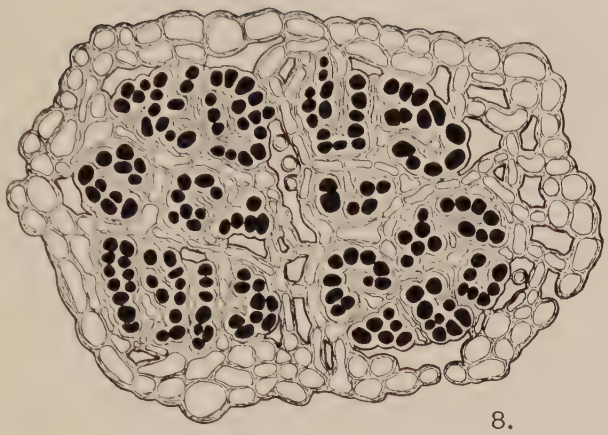

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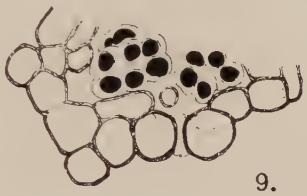

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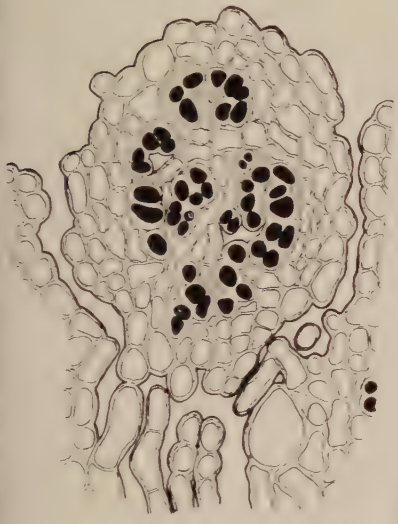

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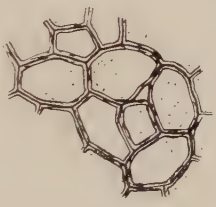

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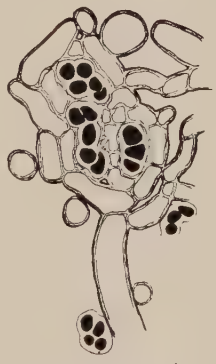

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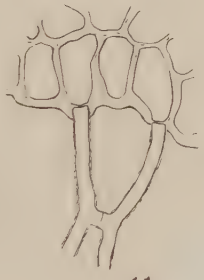

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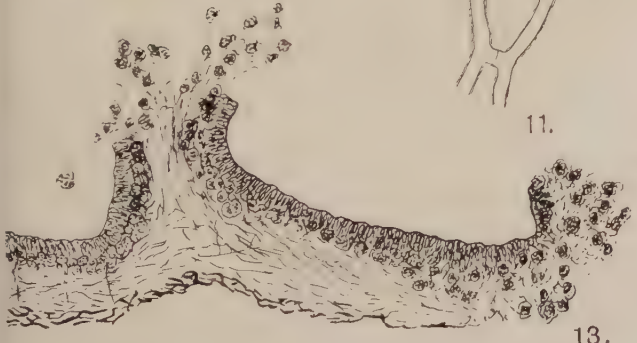

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In one branch six feet high the diseased area was not sunken, and tapered gradually towards the base, where the discoloration of the wood faded out. The bark over the faintly discoloured wood at the extreme base seemed to be healthy, though that over the more deeply discoloured wood was brown and dead. The more deeply discoloured wood contained abundant fungal hyphae, and from it *Diaporthe* and several other fungi were isolated; but in the faintly discoloured portion of the wood only a very few extremely fine hyphae could be made out. From this basal part only *Diaporthe* was isolated.

Bacteria were never encountered below the sunken areas on the lilac branches.

The fungus had evidently gained access to the wood at the extensive wounds made five years ago when the lilac bushes in this garden had been pruned hard back.

When the diseased branches were surface-sterilised and kept in a moist chamber, pycnidia or perithecia of *Diaporthe* appeared, often in a few days. As found by Miss Cayley, some strains of the fungus gave perithecia only, while others gave only pycnidia. Even in naturally infected twigs, it was found that some when kept moist produced only perithecia, while others, the majority, produced abundant pycnidia but no perithecia. Others again, produced both types of fructification.

In culture, practically no difference was observed between the lilac fungus and *Diaporthe perniciosa*, a pycnospore culture of which was kindly supplied by Miss Cayley. Ascospore cultures produced abundant perithecia with rarely a few pycnidia with undersized spores, nearly all of the "*a*" type. Pycnospore cultures, however, produced abundant pycnidia with both "*a*" spores and the filiform "*b*" spores of the same dimensions as those of *Diaporthe perniciosa*: no perithecia have been observed in these cultures.

Pycnospore cultures of the lilac *Diaporthe* regularly gave a grey coloration to the medium when grown on various substrata, a coloration which was not given by *Diaporthe perniciosa*. This was the only difference that could be observed between the two fungi. It is therefore concluded that the fungus, if not identical with *Diaporthe perniciosa*, is a very closely related form.

Inoculation Experiments.

(*a*) *On Lilac and Privet.*

March, 1925. Nine inoculations were made on lilac and five on privet (*Ligustrum vulgare*) with the lilac *Diaporthe*. T-shaped incisions were made and the bark turned back to expose the wood. The mycelium of the fungus was then inserted and the whole bound round with wool.

July, 1925. Six inoculations were made on lilac with the mycelium of the lilac *Diaporthe* in T-cuts.

July, 1925. Inoculations were made with *Diaporthe perniciosa*, three in T-cuts on lilac, using in two cases a pycnospore suspension and in the third case mycelium. Two inoculations were made on cut ends of twigs of lilac, and three on cut ends of privet twigs, with a pycnospore suspension.

These inoculations were made on twigs of one to three years old. None were successful.

(*b*) *On Peach growing in a Greenhouse.*

March 2nd, 1926. Seventeen inoculations were made with a heavy pycnospore suspension of the lilac *Diaporthe*; eleven on cut ends of twigs and six in T-cuts. The twigs used were one and two years old. No inoculations were successful. In all cases investigated of the inoculations on cut ends, a large quantity of gum was found within six weeks in the vessels below the cut surface, completely limiting the growth of the fungus. In the T-cuts examined the fungus had penetrated as far as the oldest vessels, but gum was present all round the inoculated part in large quantity and probably formed a barrier to further growth of the fungus. This barrier was similar in kind to the "gum barriers" described by Brooks and Moore(2) in unsuccessful invasions of woody tissues by *Stereum purpureum*.

February 24th, 1926. Nineteen inoculations were made with a pycnospore suspension of *Diaporthe perniciosa*. Eleven were on cut ends of twigs and four in T-cuts. None were successful.

(*c*) *On Plum growing in a Greenhouse.*

In November, 1925, inoculations were made with *Diaporthe perniciosa* on greenhouse plums by Mr F. S. Ward. Six were mycelium inoculations in T-cuts and six were pycnospore inoculations on cut extremities. Twigs of various ages were inoculated. There were no positive infections. By March, 1926, there was in all cases examined a large quantity of gum in the vessels below the fungal hyphae.

On February 24th, 1926, inoculations were made with pycnospores of *Diaporthe perniciosa*, seven in T-cuts and eight on cut extremities of twigs. The twigs used were generally one year old, occasionally two years old. No inoculations were successful. In all cases, investigated two months later, large quantities of gum were present in the vessels below the wound, and no fungus was present below the gum layer.

On March 2nd, 1926, inoculations were made with pycnospores of the lilac *Diaporthe*, three in T-cuts and nine on cut extremities of twigs one and two years old. No inoculations were successful.

In order to confirm Miss Cayley's results (3), inoculations were made in June on current year's growth of peach and plum in a greenhouse, using *Diaporthe perniciosa* and the lilac *Diaporthe*. Pycnospores in water suspension were introduced into T-cuts. None of these inoculations were successful, the growth of the fungus being limited by the rapid formation of "gum barriers."

Conclusion.

In the absence of any positive infections, the evidence for the parasitism of *Diaporthe* on lilac is as unsatisfactory as often is the case in fruit trees. From the evidence given above, however, it seems extremely likely that under unfavourable conditions for the lilac, such as dense shade, *Diaporthe* can attack the wood —at least that part which is not actively functioning. The branch is attacked on the side where no large living branches occur.

It is possible that some other fungi such as *Fusarium* may help in the attack on lilac, but the evidence for this is insufficient. In most cases investigated, the other fungi were clearly secondary whatever the *Diaporthe* may have been.

No extensive work was carried out on wound gum formation in lilac, but it was found to follow in the main the course in plum and peach as described by Swarbrick (4) and Brooks and Moore (2). The gum, however, is formed much slower and never causes so extensive a blocking of the vessels as in those plants. It seems probable that unfavourable conditions such as shade retard gum formation sufficiently for the attacking fungus to get through. Thus successive "gum barriers" may be started but may never be completed before the fungus reaches them. In this case there may be an extensive die-back. This seems to be the condition of the lilac branch described.

In conclusion I wish to express my thanks to Mr F. T. Brooks for the instigation of this work and for his assistance.

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REVIEWS.

A Monograph of Lichens found in Britain, Part II. 2nd edition, revised. By A. LORRAIN SMITH, F.L.S. pp. ix, 447. 63 plates. £1.

In the first edition of Part I of this monograph (1894) Crombie followed Nylander in his classification of Lichens. This method was to a considerable extent departed from in the first edition of Part II. In the second edition of Part I a change was again made by Miss Lorrain Smith, and a more recent classification following that of Zahlbruckner was used. In an Appendix to Part I this method was extended to the Lichens described in Part II. The new classification was used in the *Handbook of British Lichens*, 1921. We have now in these two parts of the monograph the British Lichens arranged according to the more recent methods.

In this edition there are several alterations: the genus *Gyalecta* is removed from the Lecideaceae and placed in the family Gyalectaceae, and this genus now includes the species *lutea* and *diluta* formerly placed in the genus *Biatorina*. As before the large genus *Lecidea* is divided into four sections: *Psora, Biatora, Eulecidea* and *Mycoblastus*. Following the method given in the handbook, the section *Eulecidea* is divided into two groups according to the colour of the hypothecium. Further the genera *Biatorina, Bilimbia* and *Bacidia* are divided into groups according to the colour of the apothecia. In the Pyrenulaceae an additional genus *Clathroporina* with two species follows the genus *Porina*.

In this new edition there are several alterations of specific names: *Lecidea ochracea* Wedd. is now included under *L. fuscorubens* Nyl., and *Lecidea pleiospora* A. L. Sm. is now *L. geophana* Nyl. And instead of *Verrucaria calciseda* DC. and *Thelidium incavatum* Mudd, we now have *V. sphinctrina* Nyl. and *T. Auruntii* Krempelh. Many of Dr Stirton's species still remain, though after an examination of his herbarium several have been dropped.

In an Appendix a new arrangement of the genus *Acarospora* is given as the result of an examination by Dr Magnusson of the specimens in the British Museum. And there is a list of new species of the genus *Crocynia* from a monograph on this genus by Hue and B. de Lesdain. H. H. K.

A Monograph of the Mycetozoa. By ARTHUR LISTER. Third edition, revised by GULIELMA LISTER. British Museum (Natural History). pp. xxxii, 296. With 223 plates (64 coloured) and 56 text-figs. £1. 1s. 6d.

The third edition of this monograph will be welcomed by all students of Mycetozoa. It marks a distinct advance upon the previous edition and is a worthy tribute to the combination of scientific and artistic ability of Miss Lister who has for the second time revised her father's work. When one scans the first edition published in 1894 and compares it with the present, it is surely a matter for congratulation that the study of the Mycetozoa has reached such proportions, as testified by the amount of material which has come to hand from so many and widespread localities, that such a revision is necessary.

The introduction has been carefully revised and the account of the life-history of the group brought up-to-date by the inclusion of fresh matter from the historical side and also from the biological standpoint. The reference to the work of Pinoy, and also the researches of Skupienski confirming and extending Jahn's work, and the addition of drawings made from Jahn's stained preparations will prove very helpful to the student interested in the biology of the group. With reference to the mitotic division of the nuclei in the growing plasmodium mentioned as a footnote on pp. xii and xiii, many observations made by the reviewer upon both smears and stained spreading fans of the plasmodium of *Badhamia utricularis* have always produced a negative result: there is evidently room for further research in this direction.

The inclusion of the method of collecting and mounting material should be of considerable assistance to would-be students of the Mycetozoa and forms a fitting conclusion to the introduction.

The text has undergone thorough revision and has been brought up-to-date; descriptions of three new genera have been included as well as those of forty-six additional species some of which, given as varieties in the previous edition, have been judiciously raised to specific rank. Nomenclature has occasionally been altered in conformity with the International Rules.

Twenty-two new plates have been added, eight of these being in colour from water-colour drawings made by Miss Lister. It is, however, the opinion of the writer, that several of the plates are not so well reproduced as in the second edition, e.g. *Diderma radiatum*; the difference is most noticeable in some of the black and white plates, e.g. Plates 149 and 150 and also those of *Cribraria intricata*, *C. tenella*, and *C. pyriformis*, which are very weak in tone, possibly due to the quality of the paper being inferior to that of the second edition.

Apart from these details, the new edition of this classical monograph with its extensive bibliography, the systematic side of which has been wisely separated from that dealing with the introduction, is a much needed and valuable contribution to the knowledge of the Mycetozoa, and is a testimony to the enthusiasm of Miss Lister, and a lasting tribute to her father who did so much pioneer work in attracting attention to the study of this most interesting group of organisms. H. J. H.

The Aspergilli. By CHARLES THOM and MARGARET B. CHURCH. pp. ix, 272, tt. iv, text-figs. 6″ × 9″. London: Baillière, Tindall and Cox; Baltimore: Williams and Wilkins. *22s. 6d.*

Doubtless at the present time any monograph on the genus *Aspergillus* would attract many mycologists, but the names of the authors of the work here noticed are certain to ensure for it an extensive sale. Professor Thom of the Bureau of Chemistry, United States Department of Agriculture and his assistant Miss Church by their investigation of the fungi occurring on mouldy foodstuffs and such like have established a reputation which enables them to speak with authority on the complicated taxonomy of several intricate genera of which *Aspergillus* and *Penicillium* (a monograph of which is in preparation) are well-known examples. Everyone who has attempted to identify species of *Aspergillus* knows the difficulties that are encountered. It would be going too far to say that the present monograph makes the naming of a species easy but there is so much information packed into it that one is aware of the possibilities and therefore less likely to stray.

The book is divided into two main sections. The first of these deals with matters of general biological interest—culture, physiological and biochemical characters, fermentative activities and their uses in industry; and the part played by several species in human and animal disease. Incidentally such genera as *Sterigmatocystis*, *Diplostephanus*, *Aspergilliopsis* Speg. (= *Rhopalocystis* Grove) and *Aspergilliopsis* Sopp are not upheld: the authors, moreover, do not use the name *Eurotium* for the perfect form.

The second part of the book is concerned with taxonomy. Eleven main groups are established. These "collective species" have a characteristic range of colony-colour though in some this varies with age. These are fully described from all points of view: the species which have been seen by the authors are given with morphological and historical detail while those which are regarded as synonyms or doubtful are commented upon more or less fully. The stability of the species in culture is described, how some remain constant while others saltate. There are three keys: two brief ones, of which the first is based on colour of heads and stalks, and the second a synopsis of the third detailed key which is based on general characters.

The first impression gained on dipping into the work is that it is sketchy, as if the authors had written a fair copy of their notes without any subsequent polishing. This is regrettable as it is certainly by far the most complete treatment of the genus that we have.

There are many matters which might occasion comment—and a reviewer would not be human who commented favourably on them all—but the only purpose here is to indicate the importance of the volume which everyone interested in moulds, from no matter what point of view, will need to possess. J. R.

Die Pilze Mitteleuropas. Band 1. Die Rohrlinge (Boletaceae). By Franz Kallenbach. Leipzig: Dr Werner Klinkhardt, 1926. 4 marks each Lieferung.

Under the general editorship of Professors H. Kniep, P. Claussen and J. Bass, three German scientific societies are publishing an atlas of the higher fungi of Central Europe. As is well known the late Adalbert Ricken, author of the important *Die Blätterpilze* (Agaricaceae) intended to complete his work with the consideration of the other Basidiomycetes. After his death in 1921 the Deutschen Gesellschaft für Pilzkunde took up the idea and apportioned the work to various specialists. The scheme of publication is to issue every two or three months four plates, of which two are coloured, together with the appropriate text. Two fascicles are now to hand. Plate 1 shows *Boletus satanus* (ten drawings), and Plate 2 this species with *Boletus rhodoxanthus*, *B. erythropus*, *B. luridus*, and *B. miniatoporus* (six drawings). The plates are $13\frac{1}{2}'' \times 10''$. The two black and white plates of the first fascicle (numbered 10 and 11) give fourteen photographs and one anatomical drawing. The text of four pages is devoted to a very full account of *B. satanus*: summary of original diagnosis, extended description, edible qualities, distinguishing characters, microscopic characters, habitat, distribution, history, literature and short diagnosis. The second fascicle has two coloured plates only, the first with eleven figures of *rhodoxanthus*, the second with the same number of *B. impolitus*: the text has not yet been issued. The next plates (nos. 5–9) are to show *B. pseudo-sulphureus* Kallenb., *B. pulverulentus*, *B. rimosus*, *B. erythropus*, and *B. regius*. The plates are very good of their type but heavily loaded paper printed in the three-colour process is never very pleasing. They are incomparably better than those in Ricken's work which are often said to have been badly printed on account of war conditions—but publication began in 1910 and was more than two-thirds through in Aug. 1914.

The value of the present Icones will be in the number of figures devoted to one species giving stages of development of different examples in a manner recalling Barla's *Les Champignons des Alpes-maritimes*. It is a matter of congratulation that owing to the original scheme of continuing Ricken's work the beginning is made with *Boletus* and not *Amanita*. So that even if unfortunately it should turn out that for some reason publication has to be discontinued, mycologists will have drawings of some species not previously well done. If the scheme is carried out in full (e.g. twenty fascicles for the Boletaceae alone) the Atlas will be the most complete in existence. The price is to be raised to five marks after the issue of the third fascicle. The British Mycological Society wish the German Mycological Society every success in their heavy undertaking.

J. R.

PROCEEDINGS, 1926.

MEETING, UNIVERSITY COLLEGE, LONDON. *23rd January.*

B. Barnes. Preliminary observations on the Physiology of *Lachnea.*

A. Chaston Chapman. A Plea for a National Institute of Industrial Micro-Biology.

Kodak, Ltd. The Eastman Colorimeter.

J. Ramsbottom. Fragmenta Mycologica V.

G. Tandy. Cytology of *Pyronema domesticum* Sacc.

W. M. Ware. *Pseudoperonospora Humuli* Miyabe and Tak., and its mycelial invasion of the Host Plant.

MEETING, LISTER INSTITUTE, LONDON. *20th March.*

SPRING FORAY, ARUNDEL. *21st–25th May.*

PHYTOPATHOLOGICAL MEETING, HARPENDEN. *3rd July.*

AUTUMN FORAY AND ANNUAL MEETING, HEREFORD.
27th September–2nd October.

FORAY WITH BRITISH ECOLOGICAL SOCIETY, BOX HILL.
9th October.

FORAY WITH ESSEX FIELD CLUB, EPPING FOREST. *16th October.*

AUTUMN FORAY FOR LONDON STUDENTS, VIRGINIA WATER.
23rd October.

MEETING, UNIVERSITY COLLEGE, LONDON. *20th November.*

W. R. Ivimey Cook. The genus *Ligniera.*

Prof. O. V. Darbishire. Isidia and soredia of the lichen *Peltigera.*

W. J. Dowson. An extraordinary *Botrytis* causing a disease of *Narcissus* leaves.

W. A. Roach. On the nature of disease resistance in plants, with special reference to Wart Disease of Potatoes.

A. L. Smith. A new family of Lichens.